Development of Alarm-Call Production, Usage and Responses in Meerkats (*Suricata suricatta*)

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Von

Linda I. Hollén

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SUMMARY

Despite strong selection on young and adult prey to avoid predators, we often find obvious differences in anti-predator behaviour between them. By examining the ontogeny of anti-predator behaviour, we can gain insight into how young animals come to classify predators, knowledge crucial for their survival. In this thesis, I investigated how and when young meerkats (*Suricata suricatta*) develop the ability to produce alarm calls with an adult-like structure, how they come to use these alarm calls in appropriate contexts, and how they respond to the alarm calls of other group members. Meerkats, which are cooperatively breeding mongooses living under a high predation pressure, have evolved a sophisticated alarm-call system consisting of calls which simultaneously encode information about specific predator types and the level of urgency, and calls not distinctively related to specific predator types. This system is therefore highly suitable to address questions regarding vocal development of alarm calls. Since captive environments often lack many of the natural predators that wild animals experience, research on captive animals can also offer additional insight into how experience with predators may influence a species' capabilities of responding to them. I collected behavioural observations of naturally occurring predator events, and conducted playback and manipulation experiments at different stages during juvenile development in wild and captive populations. Although young meerkats were able to respond correctly to alarm calls within three months, their probability of doing so increased as they grew older. Young were also likely to gather cues from other group members by looking towards them or running to them. These results suggest that experience is needed to perfect the alarm-call responses of young. However, young showed correct responses to alarm calls signalling predators closeby at an earlier age than to those signalling predators far away, indicating that responses may also be adapted to the level of risk posed by different situations. Correct responses were not, however, contingent upon the particular predator approaching. In terms of call production, young were less likely to utter alarm calls than were adults, but also less likely to look out for predators. Since alarm calls were more likely to be given by vigilant young, the increase in alertness with age might be responsible for an age-related increase in alarm calling. Nevertheless, alarm calls which are not related to specific predator types were produced much earlier than predator type specific calls, indicating that some learning may also be involved. Experience also seems necessary to restrict alarm calling to predators belonging to particular classes. In contrast, although the alarm calls of young underwent slight modification during development, changes which are likely to reflect physical maturation, they were more or less structurally indistinguishable from those of adult calls. All alarm calls that have been documented in the wild also occurred in captivity. The acoustic structure, however, differed slightly from that observed in the wild, but may only reflect differences in arousal. Without experience of odours from predators, captive-born meerkats distinguished between faeces of potential predators and non-predators, similar to that of wild individuals. Together, these findings show that young animals come to classify predators through a mixture of innately recognised features and gradual modification as a result of experience, and provide an important contribution to the small existing literature on predator avoidance ontogeny.

ZUSAMMENFASSUNG

Trotz starkem Selektionsdruck, potentiellen Räubern auszuweichen, unterscheiden sich juvenile und adulte Beutetiere im Räubervermeidungsverhalten. Untersuchungen zur Ontogenie des Räubervermeidungsverhaltens ermöglichen es zu verstehen, wie Jungtiere lernen, Räuber korrekt zu klassifizieren. In dieser Arbeit untersuchte ich, ab welchem Alter junge Erdmännchen (*Suricata suricatta*) die von Adulttieren bekannten Alarmrufe produzieren, ab wann Jungtiere Alarmrufe im richtigen Kontext abgeben, und wie sie auf Alarmrufe anderer Gruppenmitglieder reagieren. Erdmännchen gehören zu den Mangusten und zeigen kooperative Jungenaufzucht. Sie leben unter einem hohen Räuberdruck und haben ein hochentwickeltes Alarmsystem mit unterschiedlichen Rufen entwickelt. Diese Alarmrufe enthalten gleichzeitig Information über den Räubertyp und die Dringlichkeit. Zusätzlich gibt es aber auch Rufe, die nicht räuberspezifisch sind. Dieses System ist daher sehr gut geeignet, Fragen zur vokalen Entwicklung zu beantworten. Untersuchungen an in Gefangenschaft geborenen und lebenden Tieren können zusätzliche Information darüber liefern, wie Erfahrung die Reaktion auf Räuber beinflusst. Dazu beobachtete ich natürlich auftretende Räuber-Beute Interaktionen, und führte wiederholt Playback- und Manipulationsexperimente während der Entwicklungsphase der juvenilen Erdmännchen an freilebenden und gefangenen Populationen durch. Obwohl Erdmännchen innerhalb der ersten drei Monate sehr oft korrekt auf Alarmrufe reagierten, nahm die Wahrscheinlichkeit korrekt zu reagieren mit dem Alter zu. Jungtiere orientierten sich unter anderem auch an anderen Gruppenmitgliedern, indem sie diese beobachteten oder auf sie zuliefen. Diese Resultate deuten darauf hin, dass Erfahrung eine wesentliche Rolle bei der Produktion von Alarmrufen spielt. Dabei zeigten Jungtiere früher in ihrer Entwicklung situationsgerechte Reaktionen auf Alarmrufe die Räuber in der Nähe anzeigten, als auf solche für Räuber in der Ferne. Dies deutet darauf hin, dass die Reaktionen an den Grad der Dringlichkeit bzw. an das Risiko angepasst sein könnten. Korrekte Antworten waren jedoch unabhängig von dem Typ des sich nähernden Räubers. Generell gaben Jungtiere weniger Alarmrufe ab als Adulte, und Jungtiere hielten weniger Ausschau nach potentiellen Räubern. Alarmrufe wurden häufiger von aufmerksamen Jungtieren abgegeben, und die Wachsamkeit nahm mit dem Alter zu. Dies könnte den altersbedingten Anstieg in der Häufigkeit der Alarmrufe erklären. Dennoch wurden Alarmrufe, die nicht räuberspezifisch waren, viel früher abgegeben als räuberspezifische Alarmrufe. Dies deutet darauf hin, dass bei der Zuordnung des spezifischen Räubertyps Lernen und Erfahrung eine Rolle spielen. Obwohl sich die Alarmrufe der Jungtiere mit zunehmenden Alter, vermutlich aufgrund von Wachstums- und Reifungsvorgängen, leicht veränderten, waren sie in ihrer akustischen Struktur nicht klar von Alarmrufen adulter Tiere zu unterscheiden. Alle Alarmrufe, welche bei wildlebenden Erdmännchen beobachtet wurden, kamen auch bei Erdmännchen, die in Gefangenschaft leben, vor. Die akustische Struktur der Rufe unterschied sich jedoch von der wildlebender Erdmännchen, was aber auch Unterschiede in der Erregung widerspiegeln könnte. Gefangene Erdmännchen unterschieden gleich wie freilebende, zwischen Fäkalien von potentiellen Räubern und Nicht-Räubern. Diese Ergebnisse zeigen, dass junge Erdmännchen Räuber sowohl durch angeborene Fähigkeiten als auch durch zunehmende Erfahrung klassifizieren. Diese Einsichten sind ein wesentlicher Beitrag zu dem bisher wenig untersuchten Phänomen der Ontogenese des Räubervermeidungsverhaltens.

INTRODUCTION

Find that tune: how do young individuals develop the skill to produce, comprehend and respond to signals like adults do?

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….. I hope to have given you a better appreciation of our remarkable — yet largely unconscious and virtually automatic — ability to perceive one place or object or person or situation, however vast or insignificant, as "the same" as some other. It is this subtle ability, perhaps more than any other, that sets human cognition apart from any other on our planet.

R. M. French (1995)

French's anthropocentric perspective has a long history in the fields of psychology and biology, where classifying events in the external environment was long thought to be an exclusively human attribute. Detecting similarities among objects or experiences and placing them into categories have obvious advantages. By categorizing, individuals can deal with a complex world and novel situations with a minimal amount of information to remember and store. To do so, however, individuals first need to perceive the information contained in external signals, process it and then memorize it for the future, skills which require cognitive abilities thought to be absent in non-human animals. Over the years, many attempts by researchers to compare the cognitive abilities possessed by humans and that possessed by other animals have evidently shown that this is not the case.

One clear example is the debate about whether animal vocalizations could ever function referentially by providing listeners with information about external objects or events, one of the key characteristics of human speech. Historically, animals other than humans were thought to lack this capacity. In his book *The Expression of the Emotions in Animals and Man*, Darwin (1872) views animal signals as mere manifestations of emotion, only communicating a caller's motivational state. This became the general view of people for more than 100 years after Darwin expressed his ideas. Although the emotional nature of animal signals has never been in doubt, studies over the past two decades have created a more complicated picture, acknowledging that animal vocalizations, as human speech, can encode information associated with specific external stimuli, information that goes beyond the motivational state of a signaller (reviewed in Seyfarth & Cheney 2003). Following Darwin, many scientists have also shown that human speech encodes both referential and emotional information (e.g. Bachorowski 1995).

Individuals, human or non-human, are born with little knowledge about their environment and need to acquire this as they develop. Although some signals can evoke responses through reflex mechanisms, some are only of use to individuals if they have the ability to perceive it, attach a specific function/meaning to it, and subsequently respond appropriately to it. In building up learned perceptions of a particular external event, however, young must rely on a limited number of experiences, none of which are ever identical in all aspects (Marler 1982). There will always be variation, even when dealing with the same general class of objects such as food or members of one's own species. So how is it that young individuals manage to strike the fine balance of splitting and lumping experiences which they encounter, acquiring knowledge about their surrounding environment which can be crucial for their survival? Studying the development of signal acquisition and comprehension provides an insight into how this is achieved. Compared to the vast literature on speech development in humans and song development in birds, however, relatively little

effort has been dedicated to the study of vocal development in other species. Moreover, only rarely have studies considered all aspects of vocal development – signal production, usage and responses to signals of others. Below, I briefly describe general features known from other species regarding vocal production, usage and responses. I then outline why alarm calls offer a useful approach to study vocal development, provide a general background on the lives of meerkats, my study species, and finally delineate the particular questions I have investigated within my project.

Vocal production

For a long time, studies on vocal development in non-human animals focused on vocal production: the delivery of calls with a particular set of acoustic characteristics. Because of remarkable parallels in vocal production, studies on bird song development have long provided the best model for understanding the mechanisms underlying speech development in humans. The speech of children and the songs of young birds must be learnt, require practice to achieve adult form, and are strongly influenced by social interactions (Marler 1970; Baptista & Gaunt 1997; Locke & Snow 1997). In contrast, studies on non-human primates, despite being our closest relatives, have long been thought to provide no useful parallels with human speech development. This is because in terms of vocal production, calls of most monkey infants appear fully formed at birth and seem to undergo relatively little modification during development (reviewed in Seyfarth & Cheney 1997; Castro 2000). Early research on squirrel monkeys (*Saimiri sciureus*) offers a classical example of vocal production that is to a large extent genetically controlled (Winter et al. 1973). Winter and co-workers found that, in isolation-reared animals, six out of eight call types present in the monkeys' repertoire appeared on the first day of life, with acoustic structures indistinguishable from those of adult calls. A dozen other studies on non-human primates provide further evidence for vocal production with no modification during development (reviewed in Seyfarth & Cheney 1997).

In principle, vocal production that is highly heritable is possible as it occurs in for example frogs (e.g. Ryan 1988), insects (Collins et al. 1999; Saldamando et al. 2005) and some birds (Kroodsma 1984). In practice, however, it may be difficult to demonstrate, especially if some call types do not appear before young have reached a particular age. Then it is impossible to rule out that experience has played a role before the calls have appeared. Similarly, in species where young spend a few weeks below ground before emerging, one can not be certain that pre-emergent experience has not played a role (see Mateo 1996a). In fact, several recent studies adopting sophisticated analytical techniques have shown that calls exhibit greater vocal plasticity than previously thought and are by no means fixed at birth (Hauser 1989; Elowson et al. 1992; Roush & Snowdon 1994; Seyfarth & Cheney 1997; Hammerschmidt et al. 2000, 2001). Nevertheless, none of these studies have reported any substantial modification during development. Changes seem to be subtle with much of the adult-like structure already present in the calls of young, and changes that do occur are often a result of pure physical maturation (Gouzoules & Gouzoules 1989; Hammerschmidt et al. 2000, 2001). Clearly, vocal production in non-human primates seems under strong genetic control and does not show as much flexibility as is obvious in many songbirds (Marler 1990; Baptista & Gaunt 1997), humans (Locke & Snow 1997), marine mammals (Janik & Slater 1997) or even elephants (Poole et al. 2005); species which are capable of creating completely new signals, often by imitating sounds of others. However, it shows that calls are not as rigidly fixed as previously thought and it may take months or even years before the calls of young sound exactly like those of adults.

Vocal usage

In contrast to vocal production, which could potentially be under complete genetic control, there are several reasons why correct vocal usage is likely to involve at least some learning. First, environments are constantly changing and if animals use calls to signal about specific features in their environment, it is of advantage to adjust their calling accordingly. Second, many calls are only given to specific individuals, such as those of lower or higher rank (Gouzoules et al. 1984). In such circumstances, it does not make sense for vocal usage to be under strong genetic control since young individuals must learn their own ranking. Evidence from non-human primates suggests that development of vocal usage is rather a mix between non-learned and learned components (Seyfarth & Cheney 1997; Castro 2000). Young seem predisposed from birth to use specific calls in broadly defined contexts, not entirely random from that of adult usage, but over time they come to sharpen the association between call type and context. Such changes in the usage of calls have also been described as contextual learning, in which a signal already present within a repertoire comes to be associated with a new context based on experiences with how other individuals use this signal (Janik & Slater 1997, 2000). Young vervet monkeys (*Cercopithecus aethiops*), for example, show loose context specificity in the use of their intergroup encounter call, but with age come to restrict the use of these calls to encounters with other groups (Hauser 1989). By comparing monkey groups living in areas with different exposure levels of these calls, Hauser demonstrated that these age-related changes are not just due to maturational processes but contextual learning is indeed involved. Infants that were exposed to these calls more often also showed the appropriate usage much earlier than infants exposed to them at low rate. In agreement with results from field experiments, cross-fostering experiments with rhesus (*Macaca mulatta*) and Japanese (*Macaca fuscata*) macaques have shown that infants are strongly predisposed to use certain calls in specific social contexts and usage is modified only slightly, if at all, as a result of social environment (Owren et al. 1993). A partially innate ability to use calls in appropriate contexts allow young individuals to communicate more effectively with conspecifics than they would if call usage was completely random.

Responses to calls of conspecifics and other species

Perhaps one of the most striking parallels between the development of human speech and vocal development in other species is the development of the ability to respond to calls of conspecifics. In both humans and non-human animals this takes time and is to a large extent, if not completely, determined by experience (Seyfarth & Cheney 1986; Mateo 1996 a, b; Fischer et al. 2000; McCowan et al. 2001). In chacma baboons (*Papio cynocephalus ursinus*), for example, the ability to discriminate between different bark variants develops with increasing age. At an early age, infants fail to respond at all, whereas infants aged six months show adult-like responses, indicating that infants gradually learn to attach the appropriate meaning to these barks (Fischer et al. 2000). The role of learning has also clearly been demonstrated in cross-fostered young macaques, where cross-fostered juveniles show no tendency to respond preferentially to their own species calls, as opposed to the adopted species. Cross-fostered juveniles also learn to recognize individual idiosyncrasies in calls that differ acoustically from those they would normally hear, and adoptive mothers learn to attend to calls of their foster offspring (Owren et al. 1993; Seyfarth & Cheney 1997). A recent study on cross-fostered nestlings of reed warblers (*Acrocephalus scirpaceus*), dunnocks (*Prunella modularis*) and robins (*Erithacus rubecula*) also shows that although these nestlings do not develop a response to their foster species' alarm calls, learning does seem necessary to fine-tune the responses to their own species' alarms (Davies et al. 2004). Other evidence that learning is involved comes from numerous studies showing that both mammals and birds

respond to the calls of other species (Rasa 1983; Hauser 1988; Seyfarth & Cheney 1990; Shriner 1998; Zuberbühler 2000a; Ramakrishnan & Coss 2000a; Rainey 2004a, b). Responses to calls of others thus show a greater developmental flexibility than both call production and call usage. Considering that many of the species that have been investigated so far live in social groups, where young individuals must learn who belongs to their group, who have interacted with whom, whom to be submissive to etc, it is not surprising that selection has favoured a flexible link between hearing vocalizations of others and responding to them.

Using alarm calls to study vocal development

In contrast to calls given in affiliative contexts, such as contact calls or food calls, relatively few studies have looked at the vocal development of alarm calls, especially their production and usage. One likely explanation is the difficulty of acquiring such data. Alarm calls occur comparatively unpredictably, particularly in young (e.g. Seyfarth & Cheney 1980). Given their high survival benefit, however, alarm calls may be more conservative and less likely to show developmental modification (but see Blumstein & Munos 2005; Randall et al. 2005), providing useful comparisons to that of affiliative calls. Moreover, the problem of categorizing becomes most obvious in the context of predation, where the correct identification and classification of a threat may be critical for survival. A correct classification of predators may be particularly important for young individuals, who are often incapable of fast escape manoeuvres and typically display higher mortality rates than adults (Sibly et al. 1997).

Alarm calls can also provide listeners with different types of information, making them particularly interesting from a developmental point of view. In some species of birds and mammals, the alarm calls appear to provide information about the type of predator (e.g. Seyfarth et al. 1980; Gyger et al. 1987; Macedonia 1990; Pereira & Macedonia 1991; Evans et al. 1993; Evans & Evans 1999; Zuberbühler 2000b, 2001; Manser 2001; Fischer & Hammerschmidt 2001). Vervet monkeys, for example, emit three acoustically distinct alarm calls to eagles, leopards and snakes (Struhsaker 1967; Seyfarth et al. 1980). Playback experiments showed that the calls alone, without the presence of predators, elicit the appropriate responses in receivers (Seyfarth et al. 1980). These calls therefore fulfil the criteria of being functionally referential signals (Evans 1997). The vervets' categorization of predators is sensible because the different predator types demand different escape strategies in two planes (ground and trees). Thus, listening to information about what type of predator is approaching might be important because an appropriate response for one type of calls might be inappropriate for another. In species such as ground squirrels (*Spermophilus sp.*) (Robinson 1981; Mateo 1996a, b) and marmots (*Marmota sp.*) (Blumstein & Armitage 1997; Blumstein 1999), however, responses occur on a single plane since the only obvious way to escape is to run to a burrow. Since individuals principally only require information about the speed of a response, alarm calls in these species are not highly predator specific, but rather seem to convey information about the perceived urgency and risk imposed by different situations. These alarm calls are probably more an expression of the caller's fear, which varies depending on the level of urgency (Macedonia & Evans 1993; Blumstein & Armitage 1997).

The best known research investigating the development of alarm-call production and usage concerns vervet monkeys (Seyfarth & Cheney 1980, 1986). Infant vervet monkeys seem to give alarm calls that, when they first appear, are indistinguishable in acoustic properties from adult calls. However, when infants first begin to give these alarm calls, they often utter them in response to non-dangerous stimuli, such as birds (Figure 1) or warthogs (*Phacochoerus africanus*). Nevertheless, infants only give eagle alarm calls to objects in the air and leopard alarms primarily to animals on the ground (Seyfarth & Cheney 1980). These results show that, as mentioned above, the alarm calls of young are not given in an entirely

random fashion, but the range of species eliciting them is wider. It is possible that incorrect calling reflects a higher vulnerability amongst young (Cheney & Seyfarth 1981). However, since young also give alarm calls to stimuli posing no threat to them, differences between young and adults cannot be explained only in terms of vulnerability differences, leaving lack of experience as a likely explanation.

Figure 1. When infant vervet monkeys first begin to alarm call, they often give eagle alarm calls to harmless species such as small birds. Photographs: Linda Hollén.

As for alarm-call production and usage, research on the development of alarm-call responses has focused on non-human primates (Masataka 1983a, b; Seyfarth & Cheney 1986; Fischer et al. 2000; Ramakrishnan & Coss 2000b; McCowan et al. 2001), but also on ground squirrels (Mateo 1996a, b; Hanson & Coss 2001) and to a lesser extent on birds (Kullberg & Lind 2002; Davies et al. 2004; Platzen & Magrath 2005). Given the importance of escaping predation and because trial-and-error learning can be fatal, early development of appropriate responses should be under strong selection. Despite this, most studies find obvious differences in adult and juvenile responses to alarm calls, with appropriate responses developing during the first few months of life (Seyfarth & Cheney 1986; Ramakrishnan & Coss 2000b; McCowan et al. 2001). More experienced conspecifics often influence juvenile response development by acting as models for typical responses (reviewed in Griffin 2004). Juvenile Belding's ground squirrels (*Spermophilus beldingi*), for example, are more likely to respond to alarm calls if their dams are present (Mateo & Holmes 1997). There is now abundant evidence that animals can improve their responses, not only to alarm calls but to predators in general, as a result of experience (reviewed in Griffin et al. 2000).

The behaviour of young individuals may, however, not just be imperfect versions of adult behaviour but rather reflect adaptations to their developmental stage (Owings & Loughry 1985; Hersek & Owings 1994; Hoffman et al. 1999; Hanson & Coss 2001; Platzen & Magrath 2005). Such an idea seems plausible given the high vulnerability of young. The smaller size of young may make them more vulnerable to a wider range of species, so the fitness consequences of responding to stimuli which pose little threat to adults may still be less than ignoring them. Young may also suffer indirect or direct fitness consequences if their alarm calling does not evoke appropriate responses in other group members. This may be particularly important in situations when calls function to recruit other group members to threats which might be too dangerous to face alone. Studies on both non-human primates (Seyfarth & Cheney 1980; Ramakrishnan & Coss 2000b) and ground squirrels (Hanson & Coss 2001) have shown that adults respond to juvenile alarm calls with less concern than that engendered by adult calls. There may therefore be selection for a rapid onset of correct

pronunciation and usage. The idea of stage-dependent adaptations may be supported by findings which show that young can adjust their responses according to the specific risk posed by different situations or predator types. Nestlings of the white-browed scrubwren (*Sericornis frontalis*), for example, show a more intense response to parental alarm calls signalling greater threat to them (Platzen & Magrath 2005). Also, in Belding's ground squirrels, age-appropriate behaviour develops earlier in response to alarm calls signalling fast moving aerial predators than to alarm calls signalling slow moving terrestrial predators (Mateo 1996b). The differentiation between alarm calls signalling different types of threat might be a common adaptation in young animals, but few developmental studies have addressed this, even less so in terms of alarm-call production and usage.

General conclusions

Conclusive evidence from studies on non-human mammals, primates in particular, suggests that the production of calls by young individuals is to a large extent genetically controlled. The correct use of calls and the ability to respond to calls of others, however, gradually develop during the first months of life. The presence of conspecifics also seems critical in a wide variety of species. Taken together, although there are still differences between vocal development in non-human mammals, song development in birds and speech development in humans, there seems to be a general agreement that there is no longer any need to consider them as fundamentally different. If all three components of vocal development – production, usage and responses – are considered, many similarities emerge. Nonetheless, there is still a great need for studies addressing vocal development in other species than songbirds, humans and non-human primates.

Vocal development in meerkats (*Suricata suricatta*)

Study site and study species

The data for this thesis were collected from January to July 2003 and from October 2003 to June 2004 on a population of meerkats living on a 3500 hectare area of ranch-land situated along the dry bed of the Kuruman river in the southern part of the Kalahari Desert in South Africa (S26º57' E21º49'). At this site, the Kalahari Meerkat Project was set up in 1993 by Professor Tim Clutton-Brock (University of Cambridge, England). The data were collected on a range of 10-14 meerkat groups, all habituated to allow close observations from within 1 m of the animals (Figure 2). At least one individual in each group was fitted with a radio collar enabling me to find a group at any time. All animals were marked for individual identification with a subcutaneously implanted microchip, but also with hair dye or hair cuts applied to their fur to allow direct identification. These marks were applied non-invasively during sunning at the morning sleeping burrow. The life history of the majority of individuals was known since they were monitored from birth. This data were kept in a long term database, available for my use. Individuals were weighed on a daily basis using crumbs of hardboiled egg to entice them onto electronic balances. I was also able to include *ad libitum* data collected since 1999 by volunteers working for the Meerkat Project. Other than that, this thesis is the result of my own research.

Figure 2. The meerkats were well habituated to human presence. Photograph: Linda Hollén.

Meerkats are small, diurnal, cooperatively breeding mongooses living in groups of 3-50 individuals. They forage for 5-8 hours per day, digging for small prey in the sand (Doolan & McDonald 1996), a time when they often scan their surroundings for predators. Their small size and means of foraging make them particularly vulnerable to predation (Doolan & McDonald 1997; Clutton Brock et al. 1999a; Russell et al. 2002). At our study site, aerial predators large enough to prey on both adult and young meerkats are plentiful and include martial eagles (*Polemaetus bellicous*) (Figure 3), black-breasted snake eagles (*Circaetus pectoralis*), tawny eagles (*Aquila rapax*) and pale-chanting goshawks (*Melierax canorus*). The study site however lacks many large terrestrial predators due to persecution in the past, but small terrestrial predators are present and include African wild cats (*Felis lybica*) (Figure 3), caracals (*Caracal caracal*), black-backed jackals (*Canis mesomelas*) and cape foxes (*Vulpes chama*) (Clutton-Brock et al. 1999a). Other potential predators include cape cobras (*Naja nivea*), puff adders (*Bitis arietans*) and domestic cats (*Felis sylvestris*) and dogs (*Canis domesticus*).

Figure 3. Two of the main predators of meerkats, the martial eagle, and the African wildcat. Photographs: Linda Hollén.

Aerial predators, mammalian predators and snakes elicit distinct alarm calls which differ in their acoustic structure (Manser 2001). Calls given in response to snakes are also uttered when encountering deposits such as urine, faeces or hair samples of predators or foreign meerkats. These calls have been termed recruitment calls since they cause recruitment of other group members to the site (Manser 2001). Additionally, within each of these call classes, the acoustic structure of calls varies depending on the distance to the predator and the signaller's perceived level of urgency (Manser 2001). Calls given in response to predators at a far distance ('low urgency') show a tonal structure, whereas calls elicited by predators closeby ('high urgency') are much harsher and noisier (Figure 4). Typical responses to the different alarm calls are posting bipedally accompanied by visual scanning, running to a bolthole, moving below a burrow system or mobbing the predator. Experiments showed that playback of these alarm calls were sufficient to elicit appropriate responses in receivers (Manser et al. 2001, 2002). Although it has been argued that animal signals can inform listeners about both external events and the level of urgency (Marler et al. 1992; Evans 1997), meerkats provide the first firm empirical evidence that animal vocalizations encode both referential and affective information in the acoustic structure alone (Manser 2001; Manser et al. 2002). Listeners thus acquire information about both specific predators and the level of danger they represent from the calls.

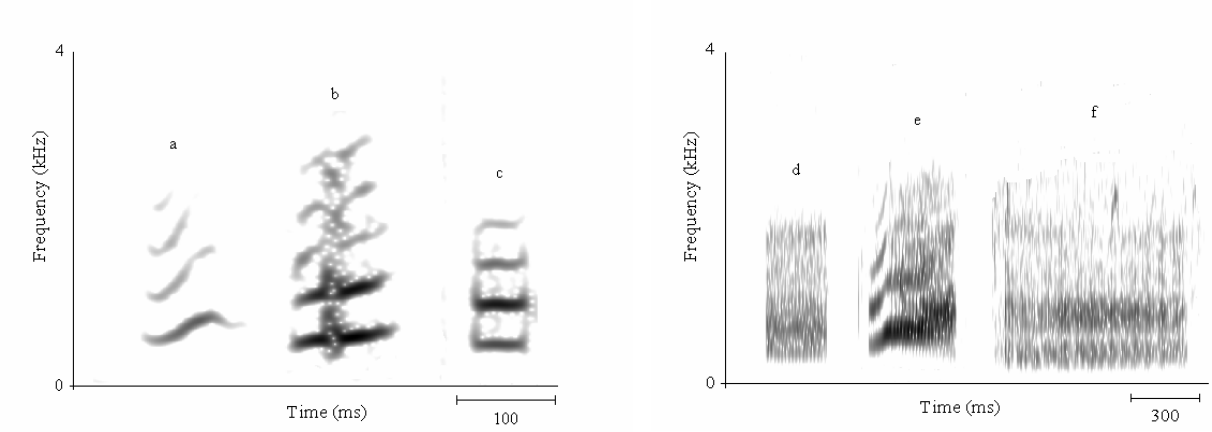

Figure 4. Spectrograms of alarm calls given in response to aerial predators at low urgency (a) and high urgency (d), mammalian predators at low urgency (b) and high urgency (e), deposits such as faeces or hair samples of predators (c) and snakes (f).

With a high encounter rate of different types of predators, and a sophisticated alarm-call system, meerkats provide an ideal opportunity to investigate how young individuals develop their anti-predator skills and what factors influence this development. Pups spend their first three weeks in the breeding burrow, during which one or several group members stay behind to guard them (Clutton-Brock et al. 1998; Clutton-Brock et al. 1999b). At around 4 weeks of age, the pups begin to forage with the group and are fed prey items by other group members until they reach nutritional independence at around 10-12 weeks of age. The peak pup-feeding period is typically between 30 and 75 days old (Brotherton et al. 2001; Clutton-Brock et al. 2001), a time in which pups remain in close proximity to other group members. Older pups, however, spend more time away from other group members, and rely on their own foraging skills. If pups use social information to acquire anti-predator skills, this change in foraging behaviour during early development may influence their ability to use such information. Young individuals, especially before 3 months of age, are particularly vulnerable and predation is the major cause of pup mortality during this period (Clutton Brock et al. 1999a). We might therefore expect that young should be strongly selected to develop their anti-predator skills rapidly, especially since older group members engage in little active defence.

Outline of thesis

In the following chapters of my thesis, I present data on the developmental patterns I found regarding the production of alarm calls by young meerkats, the use of them in their correct contexts and the responses to alarm calls of conspecifics. I show that the factors responsible for developmental changes in meerkats show striking similarities to those found in other mammals, but I also show the importance of considering specific factors that have been largely unexplored so far.

In Chapter 1, I first provide an overview of the methods used to study alarm-call communication in meerkats. I describe how we collected data using behavioural observations, manipulation experiments, playback experiments and sound recording. I also describe the methods we used to analyse the data, and aspects which are important to consider when planning and conducting field experiments. In Chapter 2, I investigated if responses to alarm calls of conspecifics change with age by comparing the responses of young and adults to naturally occurring alarm calls and playback experiments during different stages in

development. In Chapter 3, I examined whether factors in addition to age, such as vigilance level, the type of predator approaching and the distance to the approaching threat, may influence the behaviour of young, in terms of alarm-call production, usage and responses. In Chapter 4, I turn to the acoustic structure of the alarm calls uttered by young and investigate if they undergo any structural modification during development, and whether certain aspects of calls change more than others. Although studies conducted in the wild broadly reveal the natural context in which learning is useful, research on captive animals can offer an insight into a species' capabilities and behavioural flexibility in terms of anti-predator behaviour. Captive environments are often devoid of many of the natural predators that wild animals experience. I therefore took advantage of the fact that meerkats are popular animals to keep in captivity, and collected behavioural observations and conducted experiments to investigate the role of predator experience on alarm-call usage and predator recognition. These data are presented in my final chapter (Chapter 5). My thesis work provides detailed data from observational and experimental field work and makes a rare and essential contribution to the small existing literature on how young develop their anti-predator skills.

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CHAPTER 1

Studying alarm call communication in meerkats

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Studying alarm call communication in meerkats

Linda I. Hollén[1] and Marta B. Manser[1]

[1] Verhaltensbiologie, Zoologisches Institut, Universität Zürich, Winterthurerstrasse 190, 8057 Zürich, Switzerland

Abstract

Meerkats (Suricata suricatta), as many other animals, suffer from a high mortality rate due to predation. Any behaviour facilitating the avoidance of predators is therefore under strong selection. In addition to a coordinated sentinel system, meerkats have developed a sophisticated alarm call system where the acoustic structure of alarm calls provide listeners with information about both the type of predator approaching and the level of urgency. This allows receivers to respond appropriately to calls emitted in a specific context. Using a combination of behavioural observations and field experiments, our research team has investigated questions regarding alarm call communication in groups of free ranging meerkats in South Africa for the past 10 years. Our aim with this paper is to provide an overview of how we approached the study of alarm call communication. The methods we applied may also be used to investigate any other vocal communication.

Introduction

Predation is one of the major selection pressures that determine the form (Endler 1991) and behaviour of animals (Lima 1998). Any animal that possess characters or behave in a way that reduces predation risk has a greater probability of surviving to reproduction and therefore greater probability of producing offspring (i.e. higher fitness). Therefore, these characters and behaviours are under strong selection. Animals, however, face a trade-off between reducing the risk of predation and other activities important for their survival such as feeding. For example, reducing predation risk often involves scanning for predators. Although this may reduce the risk of being taken by a predator, it also reduces the time available to search for food. Essentially, any animal that maximizes its anti-predation behaviours will never be eaten, but these animals will of course starve and never have any reproductive fitness. However, whenever an animal allocates its resources to feeding instead of anti-predation behaviour its vulnerability increases. One might thus expect that animals should somehow be able to weigh the risk of predation against various benefits when deciding which behavioural option to pursue. Many studies now provide evidence that animals possess such abilities (Lima 1998).

In some social bird and mammal species, vigilance behaviour is coordinated by sentinel systems where individuals take turns in watching for predators while the rest of the group is foraging (for review, see Bednekoff 1997). It has been shown that such behaviour allow each individual to decrease its own vigilance and instead spend more time searching for food (e.g. McGowan & Woolfenden 1989; Bednekoff 1997; Manser 1999). In addition to coordinated vigilance behaviour, many group-living species also produce distinct vocalisations, called alarm calls, to warn each other about approaching danger (Klump & Shalter 1984). So far, studies of alarm calls have focused primarily on signal design and function (e.g. Sherman 1977; Klump & Shalter 1984) or the meaning contained in the alarm calls (e.g. Seyfarth & Cheney 1990; Macedonia & Evans 1993; Zuberbuhler 2000). By adjusting the behaviour according to information provided by alarm calls, animals may reduce the risk of predation.

Alarm calls potentially provide different types of information. In some species of birds and mammals the alarm calls appear to provide information about the type of predator approaching (e.g. Seyfarth et al. 1980; Gyger et al. 1987; Macedonia 1990; Pereira & Macedonia 1991; Evans et al. 1993; Zuberbuhler et al. 1997; Evans & Evans 1999; Fischer & Hammerschmidt 2001). These calls are described as functionally referential signals, meaning that they encode specific information about the eliciting event, i.e. they provide information about events in the external environment (for review, see Evans 1997). Listening to information about predator type might be important because an appropriate response for one type might be inappropriate for another. The best known example of functionally referential alarm calls is that of vervet monkeys, *Cercopithecus aethiops*, (Seyfarth et al. 1980). Vervet monkeys emit three acoustically distinct calls to eagles, leopards and snakes. Playback experiments showed that the calls themselves without the presence of a predator elicited the appropriate response by receivers. Their categorization of predators makes sense because these different predators demand a different kind of response. In species such as ground squirrels (Robinson 1981; Mateo 1996a, b) and marmots (Blumstein & Armitage 1997; Blumstein 1999) where the only obvious way to escape is to run to a burrow, alarm calls are not highly predator specific but seem to convey information about the perceived urgency and risk in the situation. This makes sense since they principally only require information about the speed of response. Some authors have argued that these alarm calls are probably more an expression of the caller's fear, which varies depending on the level of urgency (Macedonia & Evans 1993; Blumstein & Armitage 1997). Although more recent reviews have argued that animal signals inform listeners about both external events and the level of urgency (Marler et

al. 1992; Evans 1997), meerkats (*Suricata suricatta*) provide the first firm evidence that animals signals are capable of encoding both referential and affective information in their acoustic structure alone (Manser 2001; Manser et al. 2002).

Meerkats are diurnal, small cooperatively breeding mongooses inhabiting the semi desert regions of Southern Africa (Clutton-Brock et al. 1998). The group, ranging in size from 3-47 individuals, typically comprise a dominant male and female breeder (who account for the majority of pups born, Griffin et al. 2003) and their retained offspring of both sexes and various ages. Dominant females can give birth to three to four litters per year with typically three to seven pups per litter. Pups spend their first three weeks underground and when they are approximately four weeks old they begin to follow the group on foraging trips (Clutton-Brock et al. 1999a). Meerkats forage for several hours per day, digging for small prey in the sand (Doolan & McDonald 1996). During foraging they frequently scan their surroundings for predators and although predation is seldom observed, their small size and means of food acquisition makes them highly vulnerable to predation (Doolan & McDonald 1997; Clutton Brock et al. 1999b; Russell et al. 2002). Meerkats are preyed upon by several aerial and terrestrial predators, including snakes, and have developed an alarm call system that simultaneously encode information about both predator type and the signaller's perception of urgency (Manser 2001, see Fig. 1). When encountering snakes or deposits such as urine, faeces or hair samples of predators, alarm calls are used to recruit other group members to the site. Adult meerkats effectively classify alarm calls and respond differently depending on which alarm call is given (Manser et al. 2001). Typical responses are posting bipedally accompanied by visual scanning, running to a bolthole, moving below a burrow system or mobbing the predator (Manser et al. 2001, see Box 1). Pups on the other hand gradually develop the correct responses to these different alarm calls (Hollén, L. & Manser, M.B., unpublished data).

Over the past 10 years, we have been interested in answering questions like: 1) How many different types of alarm calls do meerkats use? 2) What information do alarm calls contain? 3) How do individuals respond to different alarm calls 4) What factors, such as sentinel behaviour and the presence of pups, affect their alarm calling behaviour? and 5) How do young meerkats develop the ability to produce and respond to alarm calls correctly? Our aim with this paper is to give a general overview of how we approached the studying of alarm call communication in meerkats. We do not however intend to give a detailed description of the equipment we used or the technical details on how to use them. We will in particular focus on the use of (i) behavioural observations, (ii) manipulation experiments, (iii) sound recordings, and (iv) playback experiments. We will also briefly mention the analysis methods we used, including video and acoustic analysis, and aspects important to consider when planning and conducting field experiments.

Methods

Study site and population

Our research is taking place at the Kalahari Meerkat Project, run by Professor Tim Clutton-Brock, University of Cambridge and Professor Marta Manser, University of Zürich. The project is running since 1993 and is well established with 10-14 study groups. The study site is located on a 3500 hectare area of ranch land situated along the dry bed of the Kuruman river in the southern part of the Kalahari desert in South Africa (S26º57' E21º49', for details, see Russell et al. 2002). Although all large terrestrial predators have been eliminated from our study area, there are plenty of potential predators around. Small terrestrial predators are present and include African wild cat (*Felis lybica*), caracal (*Caracal caracal*), black-backed

jackal (*Canis mesomelas*) and cape fox (*Vulpes chama*) (Clutton-Brock et al. 1999b). Raptors are more abundant and include the martial eagle (*Polemaetus bellicous*), black-breasted snake eagle (*Circaetus pectoralis*), tawny eagle (*Aquila rapax*) and pale-chanting goshawk (*Melierax canorus*) (Clutton-Brock et al. 1999b). Data on the encounter rate of different predators has been collected since 1996.

All of our study animals are habituated to human presence, allowing very close observation (< 1m). To enable study groups to be located, one individual in each group is fitted with a radio collar (Telonics Telemetry Electronics Consultants). All individuals are marked for individual identification with hair dye or hair cuts applied to their fur. These marks are small and applied non-invasively during sunning at the morning sleeping burrow. When pups first emerge from their burrow they are implanted with a small subcutaneous transponder chip. This is to ensure that all animals can be correctly identified if there is any ambiguity over identity. Ages of individuals are known precisely because their development has been monitored since birth. Furthermore, all individuals can be weighed repeatedly each day using top-pan balances (see Russell et al. 2002), allowing us to investigate the effect of body condition on anti predator behaviour.

Behavioural observations

Behavioural observations are an important component when studying communication, providing information on which further experiments can be based on. We collected data on alarm call production and responses to naturally occurring predator encounters while walking with the group using an *ad libitum* sampling procedure (Martin & Bateson 1993). Ad lib observations concentrate on sporadic behaviours of the whole group. On a typical day, foraging groups were followed from emergence from their sleeping burrow until foraging behaviour ceased around midday (~ 3-4 hours). In the afternoon, we located the group and followed them until they entered their sleeping burrow at sunset (~ 2-3 hours). We collected data using a Visor Pro handheld computer (palmOne, Inc., Milpitas, USA) or a PSION datalogger, organizer II, model LZ64, which allowed us to transfer our files directly on to a computer. Whenever an alarm call was emitted we recorded: (1) the identity of the first animal emitting the alarm call, (2) the type of alarm call emitted, (3) the stimulus eliciting the alarm call, (4) the estimated distance to the stimulus, (5) the behavioural response shown by the majority of the group (> 50% of the group members). Responses were classified according to standard codes used by all field assistants at the Kalahari Meerkat Project (see Box 1), (6) the distance from the caller to the nearest neighbour, (7) the distance from the caller to the nearest pup and (8) the distance from the caller to the nearest bolthole or burrow system.

Calls were categorized depending on (i) whether they were elicited in response to aerial or terrestrial predators, snakes or deposits, and (ii) the distance to the predator (for details, see Manser 2001). Calls elicited in response to snakes or deposits were defined as recruitment calls since they typically caused the recruitment of other group members to investigate the stimuli. The distance to the eliciting stimuli was visually estimated but only used in the analysis for aerial and terrestrial predators. This is because calls emitted in response to snakes or deposits always occurred within a very short distance of the stimulus. Distances for aerial and terrestrial predators were standardized to different levels of urgency, where predators at a far distance were labelled as low urgency and predators at a close distance as high urgency (for details, see Manser 2001). For recruitment events, calls elicited in response to deposits were defined as low urgency while encounters with snakes posed a high urgency situation. Box 2 provides information on what is worth considering during natural observations of predator encounters.

Box 1. ***Response codes used at the Kalahari Meerkat Project***

No response: When a predator is sighted but do not elicit any response or when a predator is sighted by the observer but not by the meerkats

Look briefly: When meerkats only look up briefly and resume foraging behaviour shortly after

Watch continuously: When meerkats observe the predator for a longer time

Move: When meerkats move a short distance but do not run to a bolthole (shelter)

Move to bolthole: When meerkats move to a bolthole

Move below: When meerkats move to a bolthole and disappear below ground

Mob: When meerkats gather together and with tails erect mob the predator, for example snakes or scents

Box 2. ***Worth considering when conducting behavioural observations***

- There are a few problems with visual estimation of distance. One is the potential lack of accuracy, especially for aerial predators far away. Another one is a potential observer bias. When we compared distance measurements from different observers, there was a substantial amount of variation between them. To minimize possible observer errors, we did not use the absolute distance in our analyses but instead used distance categories. Perhaps an even better solution, at least for predators approaching on the ground, would be to use a laser range finder. These range finders can usually estimate the distance to an object up to about 1.5km. It may still be difficult to use range finders on moving objects in the sky.
- It is worth thinking carefully about what statistical methods you want to apply. With observational data we often end up with categorical data to analyse. This is normally not a problem but if you have many confounding variables to take into account, such as the random sampling of specific individuals or groups over time, you need to use a mixed effects model procedure when analysing your data. With categorical data this proves to be slightly difficult but is now possible with improved statistical software. Recommended software to use is R for Windows (freeware available for download at http://www.r-project.org) or S/S-plus (license needed, see http://www.insightful.com). For mixed effects modelling using these programs, see Pinheiro & Bates 2000.

Manipulation experiments

To further investigate the alarm call production and perception, Manser (2001) performed several manipulation experiments. Manipulation experiments allow testing responses to specific stimuli under controlled conditions, where other factors are kept constant. Also, the responses of specific target individuals can easily be investigated. Furthermore, these experiments provide a useful tool to increase sample size for infrequently occurring events. However, as described for playback experiments (see Box 4), the frequency of such experiments has to be kept low and appropriate control experiments have to be conducted under the same conditions.

A terrestrial intrusion was simulated by exposing the meerkats to stuffed predators and a dog held on a leash. Stuffed specimens of honey badger (*Mellivora capensis*), black backed jackal, and caracal, were mounted on a plastic frame and pulled towards the group. The frame was pulled by a fishing line at a constant rate and passed the group at 8-10 meters distance. The dog, held by an observer, was walked past the group and to control for a potential reaction to people, control experiments where the observer alone approached the group were conducted. Making sure the animals are habituated to walking people is important when exposing them to predator models accompanied by observers. A kite shaped and painted like

a martial eagle, as well as a remote controlled aeroplane with the size and colour of a martial eagle, were used to simulate an aerial predator approaching. To control for the noise of a remote controlled aeroplane, experiments with only noise were conducted. The responses to the intruders were filmed with a digital camera and alarm calls recorded with a DAT recorder connected to a Sennheiser directional microphone. To investigate the function of recruitment calls and mobbing behaviour, meerkats were recently (in 2004) presented with live snakes, kept in a well protected cage (Graw, B. & Manser, M.B., unpublished data).

In addition to direct encounters with predators, animals can gain information about their presence by inspecting secondary cues such as urine, faeces or hair samples. The use of olfactory cues to detect predators has been described in a variety of studies (e.g. Randall et al. 1995; Ward et al. 1997; Amo et al. 2004). To investigate how meerkats respond to secondary cues of predator presence, we presented them with a small sample of African wildcat hair. The hair was cut out from salt treated skin, which was kept in a freezer for preservation. As a control experiment we presented them with Cape ground squirrel (*Xerus inauris*) hair, gained from road-kill carcasses. A new sample of hair was taken out of the freezer before each presentation, and kept cold in the field until the experiment started. In addition, if hair was presented multiple times during one session, a new sample was used for each presentation. This is because reusing a sample after it has been sniffed by an animal might affect subsequent responses by other animals. The hair was placed in the foraging path of the focal individual when no other individuals were closeby, and responses were videotaped. In the same way we tested the responses to owl pellets and urine and faecal samples of predators and conspecifics. A positive response typically resulted in recruitment of the rest of the group. Videotapes were then analysed using frame by frame analysis (25 frames/s) in Windows Movie Maker version 5.1. We obtained the following response measurements: (1) the number of approaches to the stimuli, (2) the number of times an animal investigated the stimuli, (3) the total inspection time, (4) the type and length of alarm call given, (5) if calls emitted resulted in recruitment of others, and
(6) the time spent scanning the surrounding.

Sound recording

The information contained in the acoustic structure of alarm calls was studied by recording alarm calls occurring during both natural predator encounters and manipulation experiments. Calls were recorded at a distance of one to two meters from the caller, using a Sony digital audio tape recorder DAT-TCD D100 (Sony Corporation, Tokyo, Japan) with 90 min DAT tapes (TDK DA-RXG) or a solid state recorder Marantz PMD 670 (New York, USA) connected to a Sennheiser directional microphone (K6 power module and ME66 recording head with a MZW66 pro windscreen; frequency response 40–20,000 Hz ± 2.5 dB, Old Lyme, CT, USA). Audio DAT tapes were uploaded in real-time to a PC notebook and digitized (16-bits, 44 kHz) using a 24-bit U24 waveterminal USB audio interface (Ego-sys, Seoul, Korea). The Marantz recorder was connected to the computer via the USB port (see Box 3). To create a library of calls, we transcribed the audio files by using a programme called Transcriber (developed by Linguistic Data Consortium, University of Pennsylvania). This programme can be downloaded at http://www.ldc.upenn.edu/mirror/Transcriber. The developers can be contacted if it is necessary to adjust the programme for your own needs (for picture of the meerkat version, see http://www.ldc.upenn.edu/sb/meerkat.gif). To extract calls for acoustic analyses, spectrograms were visually inspected using Cool Edit 2000 (Syntrillium Software Corporation, Phoenix, USA) and only calls with a high signal to noise ratio (i.e. low background noise) were chosen. Acoustical analyses were performed using Avisoft-SASLab Pro 4.33c (Avisoft Bioacoustics, Berlin, Germany) and LMA 9.2 (developed by K. Hammerschmidt). LMA is a software tool to extract sets of call parameters from complex

acoustic signals (Schrader & Hammerschmidt 1997). To determine whether alarm calls could be assigned to different contexts (i.e. predator type and urgency level) according to their acoustic structure, a discriminant function analysis (DFA) was performed. DFA analysis provides a classification procedure that assigns each call to its appropriate group or to another one. For information on what is worth considering when recording sound, see Box 3.

Box 3. ***Worth considering when recording sound***

- Although the DAT recorder has been extensively used in the field of acoustics, the Marantz solid state recorder is becoming more and more popular. The Marantz has the advantage of recordings being immediately saved on a compact flash memory stick as already digitized uncompressed wave files. Therefore, it can be plugged directly in to the USB port of a computer.
- With any equipment one uses, an important point to remember is that the quality of a recorded signal depends on a a number of factors, such as the distance and position to the recorded animal. For example, being too close to the animal can cause over distortion in the signal (for details on properties of animal sound and how to record it, see Bradbury & Vehrencamp 1998).
- Also remember to speak on to the tape what is happening but be careful not to speak too much as that will interrupt the calls. If two channels are available on your recording equipment, it is recommended to use one channel for the recording of the animal and the other channel for the recording of comments.
- It is highly advisable to transcribe audio files immediately after coming back from the field. Otherwise a stack of recordings will build up and there might not be enough time to go through them all.
- Because of high sensitivity to sand, dust and humidity, it is important to keep recording equipment well protected, especially when working in a desert environment or humid habitat. We also experienced deterioration among our audio tapes, especially when reusing old ones. This might be because of heat sensitivity and one solution could be to keep them in a cool storage space.

Playback experiments

One of the most useful tools for studying communication and cognition of animals is the playback experiment. In these experiments, researchers use a hidden speaker to play back a recording of an animal's call to other animals. How animals respond to playbacks can help researchers understand things such as the meaning of different calls, how animals respond to predators, and how animals defend their territories.

In meerkats, alarm calls used in playback experiments were obtained from sound recordings during naturally occurring predator encounters. Natural call sequences of good quality (i.e. high signal to noise ratio) were prepared using Cool Edit 2000. Cool Edit is an extremely user friendly programme where calls can easily be cut out from one sound file and pasted in to a new sound file, several filter methods are available and the amplitude of calls can easily be adjusted. Playback calls were recorded back from the computer onto a DAT cassette tape or the Marantz recorder for use in the field. Calls were played from the DAT or Marantz connected to a loudspeaker (Sony SRS A60) and responses filmed with a digital video camera (Sony DCR-PC 120E). The target individual was filmed for at least 20 seconds before the call was played and until normal foraging behaviour was resumed. The loudspeaker was hidden behind vegetation five to ten meters from the focal individual and calls were played when the individual was at least five meters from a bolthole, and not engaged in vigilant behaviour. Calls were only played if there had not been a natural predator encounter during the preceding 20 minutes since this might affect an animal’s response. Playback

experiments were conducted during both morning and afternoon foraging sessions. To minimise habituation to playback experiments (see Box 4), we kept the amount of playback experiments below the natural rate of alarm calling. In each group, a maximum of two playback experiments were conducted per day with at least one hour in between. In addition, at least five days passed between successive playbacks in each group. To avoid pseudoreplication (see Box 4), we used several different examples of each call type being played back. We also minimized a possible influence of age related differences in acoustic structure by only using calls emitted by adults. Since bird song is frequently heard in the area, songs from two different species, Whitebrowed sparrow weaver (*Plocepasser mahali*) and Kalahari scrub-robin (*Cercotrichas paean*) were included as control stimuli. Control playbacks were also performed by broadcasting the 'close' call, vocalisations continuously emitted by meerkats while foraging (Manser 1998). The volume of the calls was adjusted to the amplitude observed during naturally occurring predator encounters using a Tandy sound pressure level meter.

When back from the field, videotapes were uploaded on to a PC computer and responses quantified using frame by frame analysis (25 frames/s) in Windows Movie Maker version 5.1 (included in Windows software). Although analysing videotapes is time consuming, the advantage is that recordings can be viewed in slow motion, and detailed behaviour that can not easily be picked up by observations alone can be analysed with high accuracy. Despite being a very useful tool when studying communication, playback experiments are prone to a number of problems. For a brief summary of potential problems, see Box 4, but for more detailed reviews and potential solutions, see Hurlbert (1984), McGregor et al. (1992), McGregor (2000), Kroodsma et al. (2001) and Wiley (2003).

Box 4. *Potential problems with playback experiments*

Pseudoreplication

Was first defined by Hurlbert (1984) as 'the use of inferential statistics to test for treatment effects with data from experiments where either treatments are not replicated or replicates are not statistically independent'. McGregor et al. (1992) provided a simpler explanation: 'the use of a sample size in a statistical test that is not appropriate to the hypothesis being tested'. Pseudoreplication can consist of repeated presentation of the same stimulus, repeatedly using the same subject, or pooling results from presentations of similar stimuli.

Biological and statistical independence

Biological non-independence can occur when one subject's response influences another subject's response. An example is if a subject receives two presentations, its response to the second might be influenced by the response to the first. Important compensations for possible biological interactions are randomization and permutation of the order of presentation. Statistical independence (as defined by Hurlbert 1984) requires that the values of any observations are not a condition of the values of any other. Lack of statistical independence can occur if for example one treatment is applied to one set of subjects and another treatment applied to a second set of subjects at a later time. Even if subjects are biologically independent, if for example seasonal changes affect subjects' behaviour, the observations might lack statistical independence.

External validity

Concerns the generalizability of the experimental results to what is happening in the real world. For example, only using one example of each stimulus class does not provide a great external validity (Wiley 2003).

Sample size

Choice of sample size requires compromises. Although a large sample size permit detection of smaller differences between treatments, they can also reveal small systematic biases. Field experiments, generally, should seek large effects with simple designs and smaller samples (Wiley 2003).

Habituation

Too many playback experiments on the same subject or on the same day may cause animals to habituate to the experimental setup or the observer performing the experiment. This may influence their response and interpretation of the results. It is difficult to predict how far apart in time two experiments should be. However, as a general rule, experiments should not be performed more frequently than naturally occurring encounters with the particular stimuli being tested.

Quality and loudness

Calls used in playback experiments should contain as little background noise as possible, in particular loud bird noise or technical noise (distortions). An experimenter also has to be careful not to play calls too loud. An animal may respond only to the loudness of the call and not to the other particular features of the call.

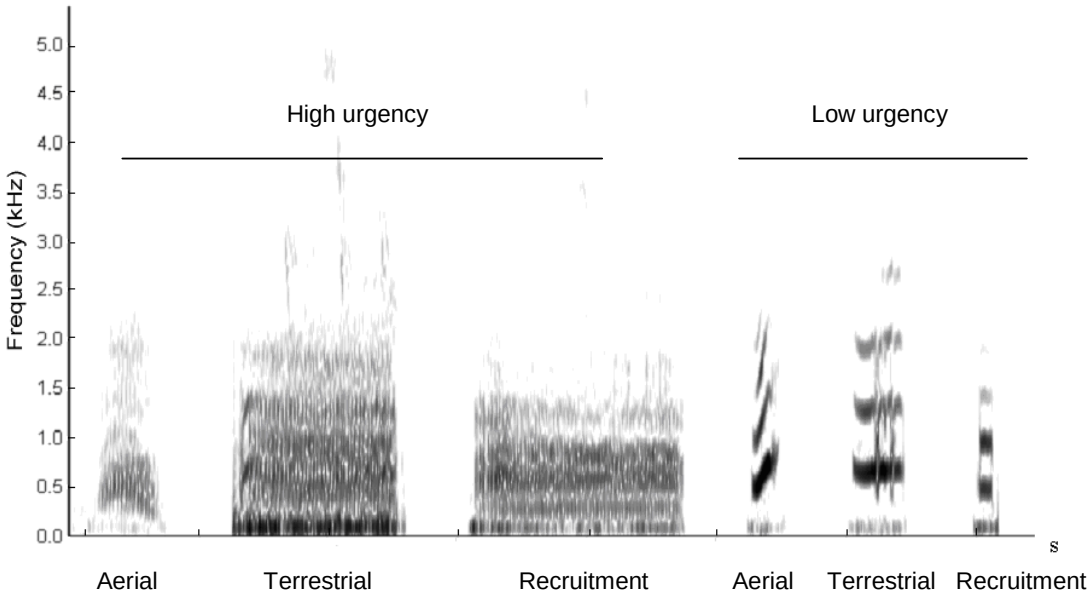

Figure 1. Spectrogram of the six most commonly used alarm call types in our playback experiments. Different call types are emitted in response to aerial and terrestrial predators as well as recruitment events (encounter with snakes or foreign scents). Within each call type, the acoustic structure changes with the level of urgency.

Conclusions

Studying both alarm call production and responses to alarm calls is required for a complete understanding of the ways in which a species use these calls to communicate about danger. Studying alarm call production is also crucial in order to design playback experiments and to interpret their results. The approach we took is based on methods that have been widely applied to the study of alarm calls in many different species of non-human primates, ground-dwelling sciurids and to a lesser extent birds, and may of course also be applicable to other taxa when investigating similar questions in acoustic communication. The study of alarm call communication, if carried out thoroughly and with proper experimental design, can provide useful insights into the meaning of animal signals and the ways in which nonhuman animals classify objects and events in the world around them, a skill long thought to be an exclusively human attribute.

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CHAPTER 2

Ontogeny of alarm-call responses in meerkats, *Suricata suricatta*: the roles of age, sex and nearby conspecifics

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Ontogeny of alarm-call responses in meerkats, *Suricata suricatta*: the roles of age, sex and nearby conspecifics

Linda I. Hollén[1] and Marta B. Manser[1]

[1] Verhaltensbiologie, Zoologisches Institut, Universität Zürich, Winterthurerstrasse 190, 8057 Zürich, Switzerland

Abstract

Given the strong selection on prey animals to escape predation, early development of correct avoidance strategies should be favoured. We studied the development of responses to conspecific alarm calls in a free-ranging population of meerkats in South Africa. Through behavioural observations of naturally occurring predator encounters and playback experiments, we monitored responses of young individuals from emergence (3 weeks) up to 6 months of age and compared them with those of adults (> 12 months). Although the total proportion of responses differing from those of adults was low during the observed period, the probability of responding like adults increased with age. Female young, who remained in closer contact to adults than did male young, were also more likely to show adult-like responses. The largest proportion of non-adult-like responses was shown before reaching independence at 3 months of age and during this time, young commonly ran immediately to a nearby individual when hearing an alarm call. After playbacks of alarm calls, young also reacted more slowly, resumed foraging sooner and spent less time vigilant than did adults. We conclude that young may need experience during early development to associate an alarm call correctly with the type of threat and appropriate response. Older group members may also serve as indirect models, perhaps helping young to form this association.

Introduction

Animals are predisposed to learn about features in their environment that are relevant to their survival, but given the strong selective force that predation exerts on animals, in particular young individuals, one might expect avoidance strategies to be fully functional upon a first encounter with a predator. However, if predation risk varies in space and time (Lima & Dill 1990), or if an environmental change causes animals to be exposed to previously unfamiliar predators (Berger et al. 2001), learning would allow responses to be adjusted to local conditions. Furthermore, the protection of young from predators is an essential component of parental care (Clutton-Brock 1991), so the presence and form of parental care may influence the behaviour and survival of young. In species where parental care is present, young may rely on their parents to defend them against predators or have the opportunity to learn how to avoid them (e.g. Hodge 2003; Platzen & Magrath 2004), whereas young that do not receive parental care may be under higher pressure to have functional anti-predator behaviour from birth (e.g. Impekoven 1976; Miller & Blaich 1986; Göth 2001).

Research on the development of alarm-call responses in mammals has focused mainly on non-human primates (reviewed in Seyfarth & Cheney 1997) and ground squirrels (Mateo 1996a, b; Hanson & Coss 2001). In both non-human primates and ground squirrels, the appropriate responses to alarm calls seem to develop gradually with age, suggesting that young individuals need experience to associate alarm calls correctly with the type of threat and correct response. For example, infant vervet monkeys, *Cercopithecus aethiops*, of 3-4 months of age rarely responded like adults, whereas most infants older than 6 months did so (Seyfarth & Cheney 1986). The need for experience was further supported by Hauser (1988), who found that infant vervet monkeys exposed to superb starlings, *Spreo superbus*, alarm calls at a high rate responded appropriately to these calls at an earlier age than did infants exposed to these calls at a lower rate.

Given that learning how to avoid predators might be costly to acquire through individual experience, it is perhaps not surprising that there is substantial evidence for social influences on anti-predator behaviour in a wide range of taxa, including fish, birds and mammals (reviewed in Griffin 2004). In addition to observational conditioning (Cook et al. 1985), where individuals acquire alarm responses to previously neutral stimuli, the exposure to alarm behaviour of conspecifics can also enhance the specificity of juvenile responses (Seyfarth & Cheney 1986) or cause correct responses to develop more quickly (Mateo & Holmes 1997).

In contrast to studies on human language development (e.g. Galsworthy et al. 2000; Berglund et al. 2005), differences in communicative skills between the sexes have received comparatively little attention in studies of animal vocal development (but see Gouzoules & Gouzoules 1989; Yamaguchi 2001). To our knowledge, studies on the development of alarm-call responses have not looked specifically at sex differences between young. However, this question may be important in species where survival of young differs between the sexes, such as described for meerkats, where female pups were more likely to survive than male pups (Russell et al. 2002).

Meerkats provide an excellent opportunity to investigate how young individuals develop their anti-predator skills. Pups, which are cooperatively reared by the group and remain below ground for approximately 3 weeks after birth (Clutton-Brock et al. 1999a), face extreme challenges during early development as they move from safety underground to a life above ground. First, meerkats live under high predation pressure and are preyed upon by several aerial and terrestrial predators, including snakes (Clutton-Brock et al. 1999b), so pups are suddenly exposed to a wide variety of predators and alarm calls given by older group members. Adults utter different alarm calls, eliciting different behavioural responses depending on predator type and the level of response urgency, allowing group members to

respond appropriately to calls uttered in a specific context (Manser 2001; Manser et al. 2001). Young individuals, especially before reaching independence at 3 months of age, are particularly vulnerable and suffer from a high mortality rate (approximately 30%) from predation (Doolan & Macdonald 1997; Clutton Brock et al. 1999b). Consequently, young should be strongly selected to respond appropriately at an early age. Second, during the first 2 months of foraging with the group (age 4-12 weeks), pups depend mainly on other group members for food (Doolan & Macdonald 1999) and therefore stay close to older individuals. Older pups, however, probably have to spend more time away from other group members because they must rely on their own foraging skills. Therefore, if pups use social information, this change in foraging behaviour during early development may also influence the acquisition and use of social information.

We investigated the development of alarm-call responses based on observations of naturally occurring predator encounters and playback experiments. We concentrated on three issues. First, we examined whether the responses to alarm calls changed with age. Second, we investigated whether the responses of male and female young differed. Third, we examined the influence of proximity to adult individuals, the number of helpers relative to the number of pups and the number of nearby individuals.

Methods

We studied the development of alarm-call responses in 11 groups of free ranging meerkats along the dry bed of Kuruman River in the southern part of the Kalahari Desert in South Africa (26º58´S, 21º49´E) from January to July 2003 and from October 2003 to June 2004 (details of study site provided in Clutton-Brock et al. 1999b). All animals were habituated to close observation (<1 m) and marked for individual identification with hair dye or hair cuts applied to their fur. These marks were small and were applied non-invasively during sunning at the morning sleeping burrow. Ages of all individuals were known because they had been monitored since birth. Pups were defined as animals younger than 3 months, juveniles as 3-6 months, sub adults as 6-12 months and adults as older than 12 months. Pups and juveniles are hereafter referred to as young. The study was conducted with the permission of Northern Cape Conservation Service and the ethical committee of Pretoria University, South Africa.

Behavioural observations

We collected longitudinal data on responses to naturally occurring alarm calls using an ad libitum sampling procedure (Martin & Bateson 1993). Whenever an alarm call was uttered, we noted the following observations on a Visor Pro handheld computer (palmOne, Inc., Milpitas, California, U.S.A.): (1) first response (within 2 s of the initial alarm) shown by the nearest young (one or several) in sight, (2) first response shown by at least half of all group members older than 6 months observed during the time of alarm (taken as a typical adult response). If no specific response was shown by more than half of the individuals, the most frequently occurring response was noted, (3) most extreme response (following the first response if response escalated) shown by young and (4) most extreme response shown by at least half of the older group members. If the response did not escalate, the most extreme response equalled the first response.

We classified responses as ‘look briefly’, ‘watch continuously’, ‘move’, ‘move to bolthole’, ‘move below ground’ or ‘mob’ (Table 1). If an individual’s behaviour did not change following an alarm call, it was scored as ‘not responding’. First responses where young looked up briefly or watched continuously were then classified as scanning the surroundings or looking towards another individual. Looking towards another individual was defined as the

young clearly focusing on an individual nearby instead of continually moving its head to follow the threat. Responses where young moved a short distance, moved to a bolthole, moved below ground or mobbed were classified as first running up to another individual (within 0.5 m) or running independently for shelter or towards threat. Finally, responses where young responded independently of other individuals, i.e. did not look towards or run to another individual, were classified as adult-like (same response as adults) or non-adult-like (different response to adults). To investigate whether the non-adult-like responses still resembled those of adults or if they differed considerably, we divided the non-adult-like responses into two categories: (1) looking responses ('look briefly' and 'watch continuously') and (2) moving responses ('move', 'move to bolthole', 'move below ground'). If the responses of young fell into the same category as the adult responses, i.e. either looking or moving, they were scored as similar; otherwise they were scored as different. We analysed 323 responses from 48 young (26 females and 22 males, age range: 19-180 days) in 19 litters and 10 groups.

Table 1. Response codes noted down during natural observations of predator encounters.

Response code	**Explanation**
Look briefly	Look in the direction of threat for < 3 sec
Watch continuously	Follow the threat continuously observing it until it has passed by
Move	Run but not all the way to a bolthole
Move to bolthole	Run to a bolthole mouth and stop
Move below	Flee down a bolthole
Mobbing	Gather around threat with erect fur and tail

Playback experiments

Recording methods and call selection

We recorded alarm calls used for playback experiments at a distance of 1-2 m from the caller, and at 44.1kHz sampling frequency, using a Sony digital audio tape recorder DAT-TCD D100 (frequency response: 20-20 000Hz ± 1 dB, Sony Corporation, Tokyo, Japan) connected to a Sennheiser directional microphone (K6 power module and ME66 recording head with a MZW66 pro windscreen; frequency response 40-20 000Hz ± 2.5 dB, Old Lyme, Connecticut, U.S.A.). Calls were uploaded on to a PC notebook and digitized (16-bits, 44 kHz) using the 24-bit U24 waveterminal USB audio interface (Ego-sys, Seoul, Korea). Natural call sequences with a high signal-to-noise ratio were then prepared using Cool Edit 2000 (Syntrillium Software Corporation, Phoenix, Arizona, U.S.A.), and recorded back on to a DAT tape for use in the field.

Behavioural responses to alarm calls vary with predator type and urgency level, so we used six alarm-call types: aerial and terrestrial calls at medium and high urgency levels and recruitment calls (elicited in response to snakes or deposits such as faecal, urine or hair samples of other meerkats or predators) at low and high urgency levels (for spectrograms and details on call-specific responses, see Manser 2001; Manser et al. 2001). We used at least six examples of each call type. To exclude any age-related differences in acoustic structure, we used only calls from adults. We used calls from both own group members and unfamiliar

individuals, because previous playback experiments have shown that meerkats do not distinguish between them (Manser 1998). Bird song is frequently heard in the area, so we included three examples from two species, the whitebrowed sparrow weaver, *Plocepasser mahali* and the Kalahari scrub robin, *Cercotrichas paean*, as control stimuli.

Experimental protocol

Responses to alarm calls without the presence of a predator were investigated by playing back calls to 11 groups. We conducted playbacks from first emergence (mean ± SD: 17 ± 2.4 days) until young reached an age of 95 days. We tested 16 randomly chosen individuals (eight females and eight males in 13 litters and nine groups) repeatedly over their development (typically every 2 weeks). These individuals received, on average, five playbacks (range 2-7) each. The low numbers of playbacks for some individuals were due to bad weather conditions, depredation or technical difficulties. Other individuals, randomly selected for each playback, were tested only once. Overall, we tested 25 females and 16 males belonging to 23 litters in 146 playbacks (including 23 control playbacks). We conducted 14 alarm-call playbacks (aerial and terrestrial medium urgency and recruitment high urgency) and six control playbacks on eight litters in seven groups during the first 2 weeks of emergence (age range: 24-30 days), when young stayed behind at the sleeping burrow together with one or several babysitters. All but one litter received multiple playbacks but with different call types. During these first 2 weeks, all pups in a litter typically stayed close together and showed the same response, so we obtained one response per litter. The remaining playbacks were conducted once young started foraging with the group (mean ± SD: 28 ± 2.6 days). Seven of the litters tested during the first 2 weeks of emergence were also tested again after foraging with the group.

Calls were played back with a Sony DAT-TCD D100 recorder connected to a Sony SRS-A60 loudspeaker (frequency response 70-20 000 Hz) and broadcast at amplitudes of 54-62 dB, measured 1 m in front of the speaker (Voltcraft 329 Sound Level Meter, Conrad Electronic, Hirschau, Germany (accuracy ± 2 dB at 94 dB)). This range of amplitudes corresponds to that observed for calls given during naturally occurring predator encounters. The duration of each playback was 3-20 s, depending on call type.

The focal pup was filmed with a Sony digital video camera DCR-PC 120E for at least 20 s before the call was played and until normal foraging behaviour was resumed after the call. The loudspeaker was hidden behind vegetation 5-10 m from the pup, and calls were played when the pup was at least 5 m from a bolthole or burrow system (after the first 2 weeks of emergence), at least 1 m from another individual and not engaged in vigilant behaviour. Calls were played only if there had not been a natural predator encounter during the preceding 20 min. To avoid habituation, the number of playback experiments was kept below the natural rate of alarm calling, and at least 3 days passed between successive playbacks in each group. A maximum of two playback experiments were conducted each day, with at least 1 h in between.

Scan sampling: proximity to adults

To investigate how the spatial relationship between young and adults changed during development, we collected data on 30 female young and 28 male young in 15 litters and 11 groups during three periods, using a scan-sampling procedure (Martin & Bateson 1993). The first period included the first 3 weeks of young foraging with the group (age range: 33-54 days; N = 12 females, 8 males), the second period included week 6-8 (age range: 70-93 days; N = 9 females, 13 males) and the third period week 11-13 (age range: 106-125 days; N = 9 females, 7 males). Each individual was used as a subject only once. We collected scans on each individual during one morning foraging session and every 15 minute we recorded the distance to the

nearest adult (<0.5 m: accuracy 0.1 m, >0.5 m: accuracy 0.5 m) on a Visor Pro handheld computer. On average, we obtained five scans per individual (range 2-6).

Data analyses

Video analysis

Responses to playback experiments were quantified from videotapes using frame-by-frame analysis (12.5 frames/s) in Microsoft Windows Movie Maker version 5.1. We obtained the following measurements for both young and adults: (1) first response (see above), (2) most extreme response (see above), (2) latency to respond (time between onset of call and first response, hereafter referred to as reaction time), (3) response duration (time between onset and end of response, which was defined as the time when normal foraging behaviour was resumed and the individual did not return to vigilant behaviour within 30 s), (4) time spent scanning the surroundings ('scanning time') after the most extreme response, if this response involved movement (scanning time for looking responses was included in response duration), (5) the distance (≤2 m or >2 m) to nearest adult and (6) number of individuals within 1 m after the most extreme response.

Reaction time, response duration and scanning time were extracted only from playbacks conducted after young started foraging with the group. The responses of young and adults may not be independent, so we also included in the analyses only those playbacks in which we could obtain measurements for both young and adults. Consequently, because we had incomplete data on adult measurements, sample size for each variable was reduced. Measurements on reaction time were extracted from 53 playbacks in 10 groups, response duration from 45 playbacks in 11 groups and scanning time from 30 playbacks in 10 groups.

Statistical analyses

All analyses were conducted using R for Microsoft Windows version 2.0.1 (R Development Core Team 2004, URL: http://www.r-project.org) and the software packages nlme (Pinheiro et al. 2004) and MASS (Venables & Ripley 2002). Where the assumptions of residual normality and variance homoscedasticity were violated, we transformed continuous variables with a natural logarithm. All tests were two tailed and based on type I sum of squares, thus controlling for preceding terms in the model. We first calculated the initial model including all explanatory variables and appropriate interaction terms. Significance level was set at $P < 0.05$, and factors with a P value above 0.10 were sequentially dropped. We examined different models using Akaike's information criterion (Pinheiro & Bates 2000). Predator type and urgency level were also included as potential explanatory variables, but these results are not presented here (L.I. Hollén & M.B. Manser, unpublished data).

We separately analysed behavioural observations, playback experiments and scans. Owing to the sampling procedure of some variables and incomplete measurements, our data were not fully balanced and sample size varies with analyses.

Behavioural observations: Unless otherwise stated, factors influencing the responses of young were analysed with a mixed-effects logistic regression model procedure characterized by a binomial error structure and logit link function. Mixed models allow both fixed and random effects to be incorporated (Pinheiro & Bates 2000; Venables & Ripley 2002). The models were fitted with penalized quasi likelihood estimation (PQL, glmmPQL function), which is a log likelihood estimation method for generalized models implemented in R (Breslow & Clayton 1993; Venables & Ripley 2002). We controlled for repeated sampling on young within different litters and groups was controlled by fitting individual identity nested within

litter and group identity as a random term. Age, sex and helper-to-pup ratio were fitted as fixed effects. Individuals over 3 months old are more or less independent, so we calculated helper-to-pup ratios as the number of group members over 3 months old to the number under 3 months old. We compared the responses of young and adults by using chi-square tests.

Playback experiments: To investigate factors influencing the reaction time, response duration and scanning time of young, we used a linear mixed-effects model procedure fitted with residual maximum likelihood estimation (REML, lme function; Venables & Ripley 2002). Group identity was fitted as a random term and age, sex, helper-to-pup ratio, the number of individuals within 1 m after the most extreme response and adult time as fixed effects. Unless otherwise stated, we also used a linear mixed-effects model procedure to compare the responses of young and adults. Playback situation nested within group identity was then fitted as a random term. This way, we controlled for repeated sampling within groups and dependencies between young and adults within each playback. Age class (young or adult) was fitted as a fixed effect. To investigate whether the proximity to adults influenced the likelihood of young looking towards others, we used a mixed-effects logistic regression model procedure with group identity fitted as a random term and age and distance to adults as fixed effects.

*Scan*s: We used a linear mixed-effects model procedure (REML) with litter identity fitted as a random term and age, sex and helper-to-pup ratio as fixed effects. Scans for each individual were pooled and the mean distance to adults was used in the analysis.

Results

Responses to naturally occurring alarm calls

Behavioural observations showed that young and adults did not differ in the likelihood of responding (responses listed in Table 1) to alarm calls (young: 89.4%; adults: 90.2%; Yates' corrected chi-square test: $\chi^2_1 = 0.02$, $P = 0.87$). However, in contrast to adults, young often responded to alarm calls uttered in response to non-dangerous birds (positive response, young: 88%; adults: 22%; $\chi^2_1 = 18.76$, $P < 0.001$) but ignored those given in response to aerial predators far away (negative response, young: 48%; adults: 9%; $\chi^2_1 = 7.16$, $P = 0.007$). However, the lack of response to aerial alarm calls never seemed to involve a great risk, because adults looked up only briefly in response to the same calls.

Young foraging with the group, especially before an age of 90 days, commonly ran to the nearest individual (42%, $N = 159$) but looked less often towards other individuals (19%, $N = 139$) when hearing an alarm call. The probability of responding independently of others increased with the age of young (running: $F_{1,124} = 11.73$, $P = 0.0008$; scan: $F_{1,105} = 4.78$, $P = 0.03$; Fig. 1a), but was not influenced by sex or helper-to-pup ratio (range of P values: 0.26-0.65).

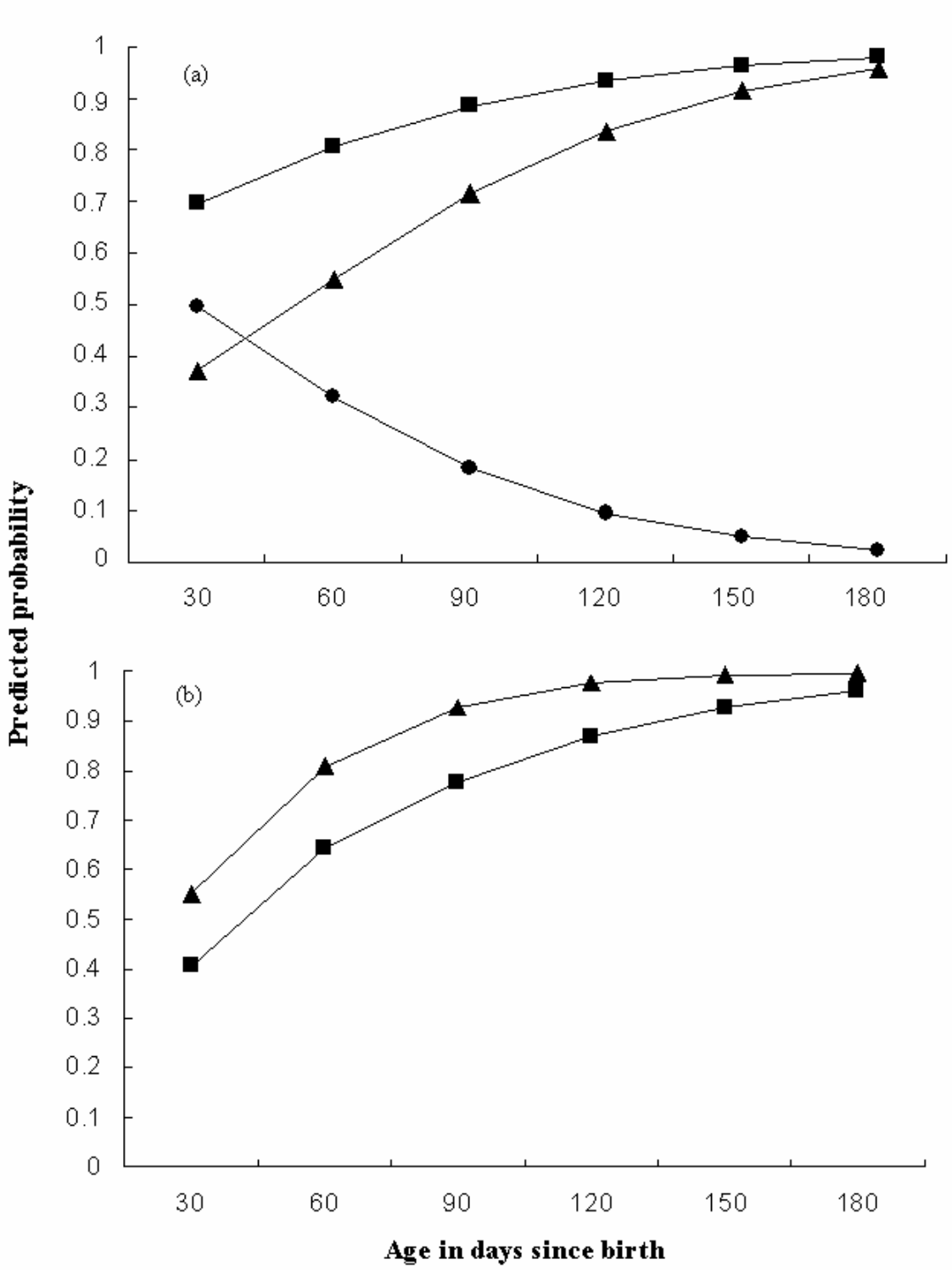

Figure 1. Fitted logistic regression curves with the predicted probability of (a) the response being independent of (▲: running; ■: scanning the surroundings) and dependent on (●) other group members and (b) female (▲) and male (■) young showing adult-like responses. Probabilities were calculated from young first foraging with the group (30 days) until reaching sub adult age (180 days).

Although a large proportion (67%, $N = 235$) of the independent responses were already adult-like, 82% ($N = 33$) of the non-adult-like responses (not responding excluded) differed considerably from those of adults (significantly different from the hypothesized value of 50%, binomial test: $P < 0.001$). Young often moved to shelter when adults looked up only briefly

(19/27 cases) or looked up briefly when adults moved (8/27). The probability of showing adult-like responses increased as young grew older ($F_{1,197} = 12.07$, $P = 0.0006$; Fig. 1b), and 87% of the non-adult-like responses were shown before an age of 90 days. Independent of age (age*sex: $F_{1,197} = 0.43$, $P = 0.51$), female young were more likely to show adult-like responses than were male young ($F_{1,197} = 5.21$, $P = 0.02$; Fig. 1b). Helper-to-pup ratio did not influence the probability of showing adult-like responses ($F_{1,196} = 0.31$, $P = 0.58$), but looking towards other individuals as a first response influenced the subsequent behaviour of young. Although only 23 of 119 most extreme responses were non-adult-like, 74% of them were shown by young responding independently instead of looking towards other individuals (binomial test: $P = 0.04$).

Responses to playback experiments

The results of the playback experiments corroborated observational data in suggesting that young and adults are equally likely to respond to alarm calls. Both young and adults responded to all alarm-call playbacks ($N = 123$) but to none of the control (birdsong) playbacks ($N = 23$). However, during the first 2 weeks of emergence, when playbacks were conducted on young and adults ($N_Y = N_A = 14$) staying behind at the sleeping burrow, all alarm calls caused the majority of young (79%) to move either below ground or closer to the entrance. In contrast, the majority of adults (79%) looked up only briefly in response to the same alarm calls ($\chi^2_1 = 7.00$, $P = 0.008$).

When foraging with the group, young commonly ran to the nearest individual but seldom looked towards others (running: 50%; looking: 23%, $N = 120$), supporting the results of observational data. Young staying further away from adults were more likely to look towards other individuals before responding than were young staying in close proximity ($F_{1,62} = 7.12$, $P = 0.01$). Again, most (82%, $N = 38$) of the independent responses were already adult-like.

Despite a strong influence of adult reaction time ($F_{1,36} = 34.79$, $P < 0.001$), young reacted more slowly than did adults ($F_{1,52} = 6.17$, $P = 0.02$, Fig. 2a). Female young tended to react faster than did male young ($F_{1,36} = 2.95$, $P = 0.09$). However, when the paired adult reaction times were controlled for, this difference disappeared ($F_{1,36} = 1.74$, $P = 0.19$). Compared to adults, young also resumed foraging faster ($F_{1,44} = 17.97$, $P < 0.001$; Fig. 2b) and spent less time scanning the surroundings ($F_{1,29} = 17.9$, $P < 0.001$; Fig. 2c). Female young resumed foraging more quickly than did male young (duration: $F_{1,30} = 5.52$, $P = 0.03$). Response duration was not influenced by adult response duration ($F_{1,27} = 1.14$, $P = 0.30$), or the number of individuals within 1 m after the most extreme response ($F_{1,30} = 2.09$, $P = 0.16$). In contrast, young increased time spent scanning with increasing adult scanning time ($F_{1,16} = 11.00$, $P = 0.004$), and tended to scan longer time with fewer individuals around ($F_{1,16} = 3.69$, $P = 0.07$). Again, when the paired adult scanning times were controlled for, this tendency disappeared ($F_{1,16} = 2.17$, $P = 0.16$). Reaction time, response duration and scanning time did not change during the first 3 months of age and were not influenced by helper-to-pup ratio (range of P values: 0.30-0.83).

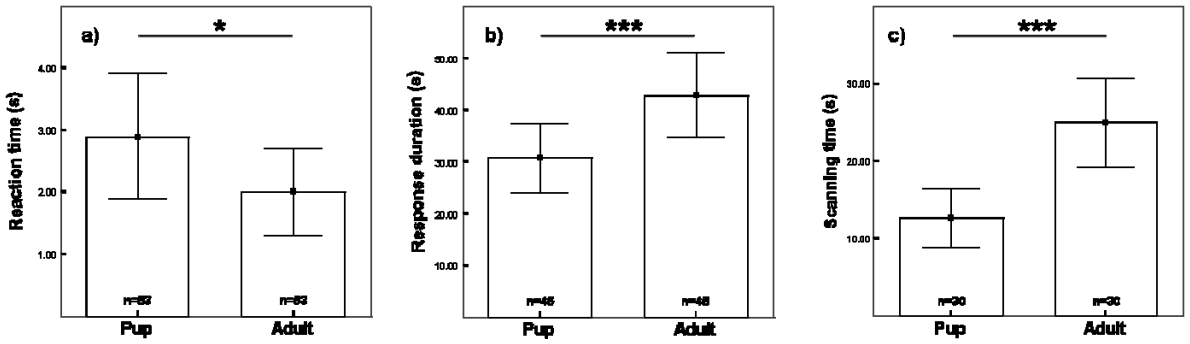

Figure 2. Differences in (a) reaction time, (b) response duration and (c) scanning time between young and adults after playbacks of alarm calls. Values are back-transformed means ± 95% confidence intervals. * $P < 0.05$; *** $P < 0.001$.

Proximity to adults

The distance between young and adults increased with the age of young ($F_{1,13} = 15.07$, $P = 0.002$; Fig. 3). Independent of age (age*sex: $F_{1,41} = 0.78$, $P = 0.38$), female young stayed closer to adults than did male young ($F_{1,41} = 5.65$, $P = 0.02$; Fig. 3). Helper-to-pup ratio did not influence the distance between young and adults ($F_{1,12} = 0.22$, $P = 0.64$).

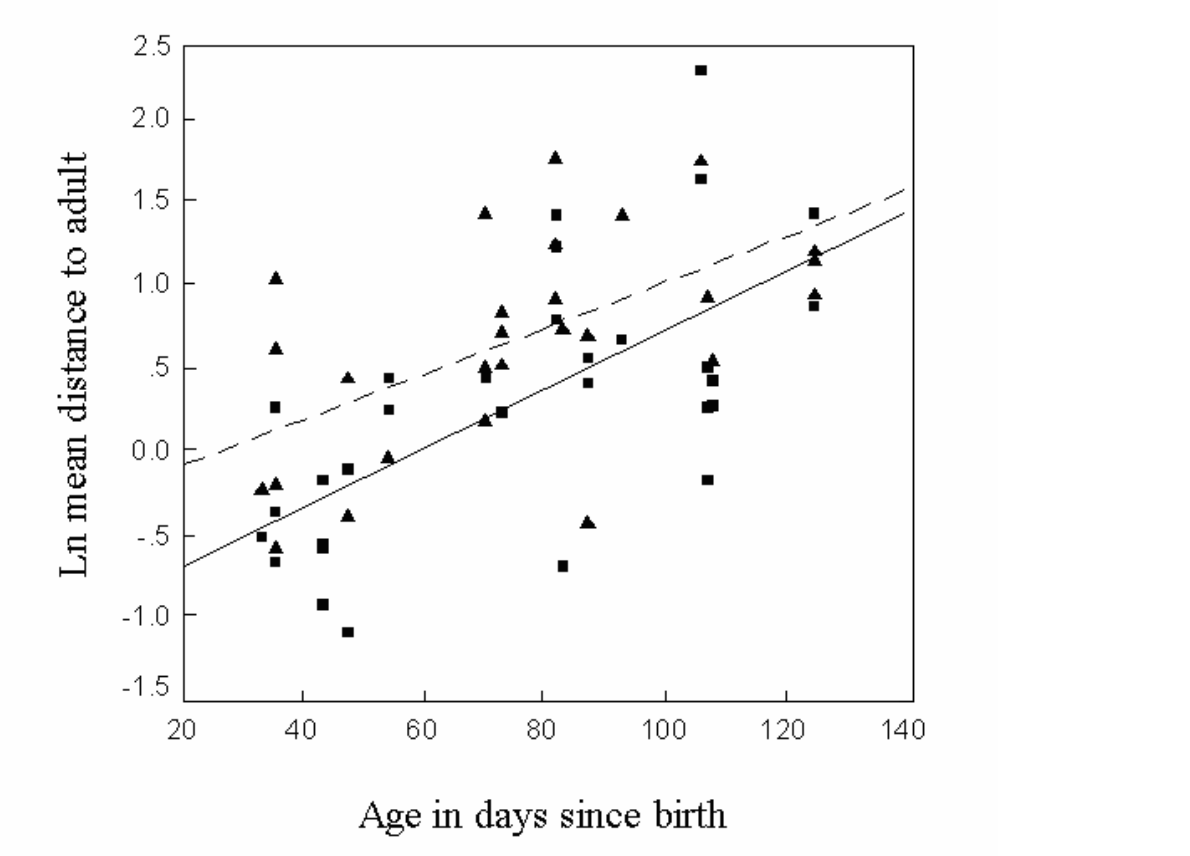

Figure 3. Logarithm of the mean distance to adults as a function of age and sex with fitted regression lines for male and female young separately. ▲, ---: Male; ■, —: female. ($R^2_{male} = 0.35$, $R^2_{female} = 0.44$).

Discussion

Although young meerkats were as likely as adults to respond to alarm calls, responses differed from those of adults in a number of ways. Unlike adults, young often responded to non-dangerous stimuli and ran for shelter when not necessary. Young also reacted more slowly and resumed foraging earlier than did adults after playbacks of alarm calls. However, as young grew older, their responses also became increasingly adult-like. Behavioural observations showed that the greatest change towards adult-like behaviour occurred before reaching independence at 3 months of age. For unknown reasons, changes in reaction time, response duration and scanning time seem to occur later. Although these results may indicate that experience is needed to adjust the responses of young, correct responses were shown early in development. One probable explanation is that, despite giving parental care, thus providing the opportunity for the pups to learn how to avoid predators, adult meerkats engage in little active defence. Thus, young meerkats may be under equally high pressure as young in species without parental care to acquire correct alarm-call responses rapidly (e.g. Miller & Blaich 1986; Göth 2001), especially because predation is the major source of pup mortality (Clutton Brock et al. 1999b).

Despite abundant evidence that animals are capable of improving their responses as a result of experience (reviewed in Griffin et al. 2000), these developmental changes could be the results of maturation rather than experience. However, the development of anti-predator behaviour is likely to be a complex process that relies on an interaction between maturational processes and learning, so it may be inappropriate to discard the role of either one of these processes. For example, newly emerged pups ignored playbacks of birdsong but behaved as though they did not discriminate between different alarm calls and entered a burrow in response to almost all playbacks. Furthermore, young foraging with the group often moved to shelter when adults only looked up briefly. This result might suggest that young are pre-disposed to recognize features of alarm calls from other irrelevant sounds, but with time they learn to discriminate between the different alarm calls and associate them with the threat that they pose (see also Davies et al. 2004). However, a simple maturational change in the discrimination threshold could also explain these results. The optimal threshold will depend on the costs of treating a non-threatening signal as an alarm or ignoring a true alarm (Reeve 1989; Sherman et al. 1997). The cost of running below ground during the first few weeks of emergence is unlikely to be high because pups remain near their sleeping burrow, but doing so may increase survival because young escape visual detection by the predator. Depending on the type of predator, foraging young may also be safer if they are already at shelter when predators approach. Therefore, lower thresholds for moving could be selected in young because of their high predation risk.

Our playback experiments also showed that young resumed foraging earlier and spent less time scanning the surroundings than did adults. Many studies have shown that juvenile mammals are commonly less vigilant than adults despite their greater risk of predation (e.g. Arenz & Leger 2000). A higher nutritional demand in juveniles (e.g. Arenz & Leger 2000), and thus strong selection on intense foraging, may lead young to rely on the vigilance of other individuals (Loughry & McDonough 1989). In meerkats, factors affecting daily weight gain are likely to be under strong selection because daily weight gain is positively related to survival throughout the first year of life (Clutton-Brock et al. 2001). The differences found between young and adults may therefore simply reflect differences in nutritional requirements, but they could also be because young are unable to assess the risk associated with the alarm calls.

In addition to associative learning, other learning mechanisms such as simple habituation and/or observational learning (Moore 2004) may be responsible for some of the observed changes in pup behaviour. First, a selective habituation process, where responses to

frequent non-predator stimuli diminish and responses to infrequent predator stimuli are maintained, could underlie the lack of responses to alarm calls given by adults in response to birds. Second, although young do not simply copy the behaviour of adults, they occasionally seem to make use of social information provided indirectly from the responses of other group members. Both the time to react and the time allocated to vigilance after playbacks were strongly influenced by adult behaviour. In addition, even though the number of adults present did not influence the behaviour of young, very young individuals in particular often ran to the nearest individual. This response is similar to that of infant vervet and squirrel monkeys, *Saimiri sciureus*, which commonly run to their mothers when alarmed (Seyfarth & Cheney 1986; McCowan et al. 2001). Looking towards other individuals was less common, but also similar to responses of vervet monkeys (Seyfarth & Cheney 1986); young doing so were more likely to show adult-like responses than young that responded independently.

Young could, however, gather helpful cues from other individuals without intentionally seeking them. First, the result that young reacted more slowly than adults after playback of an alarm call suggests that young may wait for adults to react before reacting themselves. Second, young staying further away from adults were more likely to look towards others than were young staying closer. Finally, female young, which remained in closer contact to other group members than did male young, tended to react faster and were also more likely to show adult-like responses. This result does not necessarily mean that females are generally better at responding, especially because the reaction time was strongly influenced by adult time, but young females may be more likely to gather cues from others. However, the difference in distance to adults between male and female young was fairly small, so whether this has implications for the ability to show adult-like responses remains to be thoroughly investigated.

Our results may also be compatible with a different perspective, formulated for both mammals (Owings & Loughry 1985; Hersek & Owings 1994; Hoffman et al. 1999; Hanson & Coss 2001) and birds (Platzen & Magrath 2005), suggesting that, instead of viewing the responses of young as imperfect versions of adult responses, young should be seen as adopting an optimal response for their developmental stage. The idea seems to be widely applicable, and it would not be surprising that selection may favour responses that increase juvenile survival at their current stage in development, given their high vulnerability. However, whether the behaviour of meerkat young represents age-adaptive changes or not remains an open question, because our results seem equally consistent with the idea of young showing imperfect versions of adult behaviour.

Although we cannot rule out the possibility that young could be responding directly to predators or non-dangerous birds rather than to any call uttered by other group members during natural observations, this conclusion seems unlikely where predators are concerned. First, young individuals mostly showed a response before detecting the predator themselves. Second, the results of our playback experiments, in which the presence of a predator was controlled for, corroborated those of natural observations. However, even with playback experiments, we cannot discount that young may occasionally respond to cues from other group members rather than the alarm calls themselves.

To conclude, we suggest that the observed differences in alarm-call responses between young and adult meerkats could be caused by several mechanisms (and their interactions), including maturation, non-associative learning and associative learning. Furthermore, although young may have the capacity to acquire appropriate alarm-call responses independently, our results indicate that they may gain from using cues available from other group members. Perhaps as a result of spending less time in close proximity to adults as they grow older, adult-like and independent responses emerge over development (Seyfarth & Cheney 1980; McCowan et al. 2001). Early in life, when young forage close to adults, it might be easier and safer for them to run to the nearest individual. For older individuals foraging further away from

adults, this response would be inefficient and they may be better off responding independently. These developmental trends observed in young meerkats show parallels with findings in non-human primates, ground squirrels and birds (Seyfarth & Cheney 1986; Mateo 1996a, b; Hanson & Coss 2001; Platzen & Magrath 2005), indicating that predation risk leads not only to convergence in alarm-call systems (Macedonia & Evans 1993; Evans 1997), but also to similar developmental trajectories.

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CHAPTER 3

Factors affecting the development of alarm-call production, usage and responses in meerkats (*Suricata suricatta*)

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Factors affecting the development of alarm-call production, usage and responses in meerkats (*Suricata suricatta*)

Linda I. Hollén[1], Tim Clutton-Brock[2] and Marta B. Manser[1]

[1] Verhaltensbiologie, Zoologisches Institut, Universität Zürich, Winterthurerstrasse 190, 8057 Zürich, Switzerland
[2] Department of Zoology, University of Cambridge, Downing Street, Cambridge CB2 3EJ, UK

Abstract

Despite strong selection on prey animals to correctly identify and classify predators, young individuals are often unable to do so, suggesting that experience may play an important role. Few studies have investigated whether the timing of development of correct anti-predator behaviour also varies depending on the risk posed by different situations. Here we use behavioural observations of naturally occurring predator encounters and playback experiments to examine age differences in alarm calling behaviour and the effect of both predator type and urgency level on the development of alarm-call production, usage and responses in meerkats (*Suricata suricatta*). Given that more attentive individuals might be more likely to detect predators, we also investigated age differences in vigilance behaviour. We show that both the rate of alarm calling and the amount of time spent vigilant increased with increasing age. Alarm calls associated with aerial predators, which were encountered most frequently, were produced at a younger age than other predator type specific calls. Moreover, wrong alarm calls were never emitted in high urgency situations, and young stopped showing non-adult-like responses earlier to calls signalling high urgency than to calls signalling low urgency. Our results suggest that although young meerkats are able to classify predators early on, experience combined with an increase in alertness may be important factors influencing both the production of alarm calls and the responses to them. Moreover, the development of appropriate behaviour is to some extent sensitive to the risk posed by different situations.

Keywords: Meerkats; alarm calls; ontogeny; predator-specific responses; vocal development

Introduction

As organisms learn to perceive their external environment and to act efficiently on the basis of those perceptions, they are confronted with problems of when to split and when to lump past experiences (Marler 1982). This problem becomes particularly obvious in the context of predation where the correct identification and classification of type and immediacy of a threat is critical for survival. Ignoring predators increases the probability of being caught and avoiding stimuli which pose little threat reduces the time available for other activities such as feeding (Lima & Dill 1990). Although the correct classification of predators may be particularly important for young individuals who are commonly more vulnerable and incapable of fast escape manoeuvres, young are often unable to correctly identify predators by themselves (e.g. Seyfarth & Cheney 1980; Mateo 1996a; Kullberg & Lind 2002). Studies on primates and ground squirrels have shown obvious differences in anti-predator behaviour between young and adults (e.g. Seyfarth & Cheney 1980, 1986; Mateo 1996a; Hanson & Coss 1997; Ramakrishnan & Coss 2000; McCowan et al. 2001), suggesting that specific responsiveness is something that young individuals have to learn. Examining the ontogeny of anti-predator behaviour therefore provides insights into how animals come to classify external events.

Adult individuals of many species express the categorisation of animals around them by producing specific alarm calls when encountering predators (Klump & Shalter 1984). While some species have evolved alarm calls mainly containing information about the level of response urgency, alarm calls of other species seem to rather denote the type of predator approaching (Macedonia & Evans 1993; Evans 1997). Meerkats (*Suricata suricatta*) emit both alarm calls that are not specifically related to a single predator type, and alarm calls where the acoustic structure conveys information about both predator type and urgency level (Manser 2001; Manser et al. 2001). For an individual to produce such calls and also to respond correctly to them requires that it is able to classify the situation along two dimensions: a) to recognise the type of predator and b) to estimate the level of urgency. Viewing alarm calls based on the level of urgency as an expression of motivation (Morton 1977; Marler et al. 1992), the alarm-call system found in meerkats may support the idea that predator type specific calls evolve from motivational vocalisations (Macedonia 1993). Consequently, we might expect the production of predator specific alarm calls to appear at a later stage in development, and correct responses to information related to the level of urgency to be expressed earlier than information related to predator type.

The responses of young may also be adapted to the threat posed by different predators. Yet, although it is well known that prey can show threat-sensitive predator avoidance (Lima 1998), only few studies have addressed this in terms of development. In fathead minnows (*Pimephales promelas*), naïve individuals learn to respond more intensely to predation cues associated with high risk (Ferrari et al. 2005; 2006). Similarly, nestlings of the white-browed scrubwren (*Sericornis frontalis*) show a more intense response to ground than to aerial alarm calls (Platzen & Magrath 2005). Since scrubwrens nest on the ground, ground predators pose a far greater threat to nestlings than aerial predators. Moreover, in Belding's ground squirrels (*Spermophilus beldingi*), age-appropriate behaviour develop earlier in response to alarm calls signalling fast moving aerial predators than to alarm calls signalling slow moving terrestrial predators (Mateo 1996a).

In this paper we investigate the factors affecting the development of alarm-call production, usage and responses in meerkats. Meerkats are desert-adapted mongooses living under a high predation pressure. Young, up to the age of three months, suffer from approximately 30% mortality rate due to predation (Doolan & MacDonald 1997; Clutton Brock et al. 1999a). Despite presumably strong selection on young to correctly classify predators, we previously found that although correct responses to alarm calls are present early

in development, young often gather cues from other group members and responses become increasingly adult-like with increasing age (Hollén & Manser, in press). With a large repertoire of alarm calls, including both non-predator type specific calls and predator type specific calls that simultaneously encode information about the level of urgency, meerkats provide a good opportunity to examine developmental aspects of the categorisation of their environment.

We asked whether the rate of alarm calling changes with age, and whether certain call types (non-predator type specific and predator type specific) are produced earlier than others. Comparing alarm calling between individuals of different ages however assumes that all members of a group have an equal opportunity to spot a predator. Yet, attentive individuals may more easily detect predators (Gaston 1977) and hence be more likely to emit alarm calls (Manser 1998). Therefore we also investigated whether there is a difference in vigilance behaviour between young and adult meerkats, and whether vigilance and alarm calling by young is influenced by the number of adult conspecifics present. We furthermore asked whether the following factors affect the alarm-call production, usage and responses in young: (i) the frequency of occurrence of specific predator types, (ii) the risk posed by different stimuli (vulnerability to specific predator types and predator versus non-dangerous stimuli) and (iii) the level of urgency (distance to stimuli and thus time to respond). We observed the alarm calling behaviour of young meerkats from emergence until adulthood in 13 wild but habituated groups, and tested their response to different predator type specific alarm calls with playback experiments at different ages.

Material and Methods

We collected data on a population of free ranging meerkats near VanZyl's Rus in the South African part of the Kalahari Desert (26º58´S, 21º49´E) (for details, see Clutton-Brock et al. (1999a); Russell et al. (2002)). All animals were non-invasively marked for individual identification with hair dye or hair cuts applied to their fur during sunning at the morning sleeping burrow. Animals were habituated to close observation (<1 m) and ages of all individuals were known exactly. We defined four different age categories as follows: pups, animals of less than 3 months; juveniles, 3–6 months old; sub-adults, 6–12 months old; and adults, over 12 months old. Individuals less than 12 months are sometimes collectively referred to as 'young'.

Alarm-call production and usage

To investigate age differences in the rate of alarm calling, we extracted, from a long-term database, data on which individuals gave alarm calls during natural predator encounters. For our analyses, we randomly chose 10 litters from 10 different groups, born between 2000 and 2003. During the first year of each litters life, we extracted all alarm calls emitted by young belonging to the chosen litter plus all adults (mean number of adults per group ranged from 3 to 20). We also extracted the time that each group was observed on days when alarm calls occurred, and only included days when a group was observed for one hour or more. The data collection protocol ensured that all predator alarms occurring during the observed time had been noted down. We obtained a total of 946 observation days when alarm calls occurred (range 58 – 116 days per group), and data from 43 young individuals (age range 22 – 365 days; 20 females and 23 males) and 167 adult individuals (> 365 days; 78 females and 89 males).

To investigate whether certain call types are produced earlier than others, information which is not available in the long term database, we repeatedly followed 12 litters (in 9 groups) born between January 2003 and June 2004. We collected data from pups' first emergence until they reached sub-adult age (age range 13-180 days). During this period, each litter was followed on a total of 21 ± 13 (mean ± SD) days, and visited on average once every week for an average of 3 hours per day. For the analysis, we could include 293 alarm calls from individuals less than 6 months and a matched sample of 293 alarm calls from adults. We included 11 different call types, 5 non-predator type specific and 6 predator type specific. To investigate whether young used alarm calls in the correct context, we included the calls, from these 12 litters, for which we knew the eliciting stimuli. We also included alarm calls recorded ad libitum in 4 additional groups. A total of 177 alarm calls from young and 214 from adults were included in this analysis.

We collected the data on alarm-call production and usage during naturally occurring predator encounters using an ad libitum sampling procedure (Martin & Bateson 1993). Whenever an alarm call was emitted, we noted the following observations on a Visor Pro handheld computer (palmOne, Inc., Milpitas, U.S.A.): (i) the identity of individual(s) giving the alarm call, (ii) the type of alarm call given, (iii) the stimulus eliciting the call and (iv) the estimated distance to the stimulus. We defined 4 different stimulus categories: aerial, terrestrial, recruitment events and non-dangerous birds. Aerial stimuli refer to any raptor (high risk) or vulture (low risk) approaching from the air. Even though vultures pose a low risk to meerkats compared to raptors, they occur frequently and also elicit aerial specific alarm calls (Manser 2001). Terrestrial stimuli refer to any animal (excluding snakes), dangerous or non-dangerous, approaching on the ground. We did not separate dangerous (high risk) and non-dangerous (low risk) terrestrial stimuli since most encounters were with non-dangerous animals such as herbivores. Recruitment events refer to snakes (high risk) or deposits (low risk) such as faecal, urine or hair samples of foreign meerkats or predators. Stimuli at a far distance (aerial: > 200 m; terrestrial: > 50 m) were regarded as low urgency and stimuli at close distance (aerial: ≤ 200 m; terrestrial: ≤ 50 m) as high urgency. Distance categories were not applied to recruitment events or non-dangerous birds since they usually occurred within a very short distance. However, birds and deposits typically elicited low urgency alarm calls whereas snakes elicited high urgency calls.

In addition to predator type specific alarm calls, we also distinguished between five non-predator type specific call types (Manser 2001). The first two, growl and spit calls, were often given to non-dangerous stimuli (birds, sheep etc) within a few meters of the caller. The third type, the moving animal call, was observed when animals (dangerous or non-dangerous) moved, such as horses approaching the group. The fourth type, the alert call, was often emitted only to alert other group members of raptors far away or in response to non-dangerous birds close by. The fifth call, the panic call, was given in response to birds emitting alarm calls or when aerial and terrestrial predators made sudden movements.

Vigilance

Meerkats engage in vigilant behaviour either by keeping guard from a raised position, or by frequently stopping to look around for short periods while foraging (termed "guarding away") (Clutton-Brock et al. 1999b). To gauge the effect that raised guarding has on the production of alarm calls; we extracted all raised guarding events (from the long-term database) by young and adults in the same 10 groups and over the same time periods as for the examination of age differences in the rate of alarm calling.

To investigate age differences in "guarding away" behaviour, we collected data using a focal sampling procedure (Martin & Bateson 1993). We followed each focal individual for 20 minutes and recorded the number and length of "guarding away" bouts on a Psion

Organiser II (Psion Teklogix, Inc., Ontario, Canada). We recognised "guarding away" as the interruption of other behaviours, e.g. foraging, to scan the surroundings either in a bipedal or quadrupedal position on ground level. A scanning bout was considered terminated when foraging behaviour was resumed. The duration of each bout was automatically stored by the Psion. We collected focals on randomly selected pups (N = 12, 7 females and 5 males), juveniles (N = 23, 13 females and 10 males), sub-adults (N = 16, 10 females and 6 males) and adults (N = 18, 11 females and 7 males) in 11 different groups.

Alarm-call responses

Behavioural observations

Data on responses to alarm calls were collected during naturally occurring predator encounters. In addition to stimuli type and distance to stimuli (see above) we also noted down: (i) the immediate response (within two seconds of the initial alarm) shown by the nearest pup or juvenile in sight and (ii) the most frequently occurring response shown by group members older than six months observed at the time of the alarm (regarded as a typical adult response). In addition to conspecific alarm calls, we also included responses to alarm calls given by birds (later referred to as bird alarms; most commonly given by forktailed drongos (*Dicrurus adsimilis*)). These alarm calls typically caused meerkats to run for shelter, and appeared to be perceived as high urgency situations. We were not able to include recruitment calls (in response to snakes or deposits) due to low sample size.

We classified responses in 6 different categories: "no response", "look briefly", "watch continuously", "move", "move to bolthole", or "move below ground". When young looked briefly or watched continuously, responses were further classified as scanning the surroundings or looking towards another individual (young clearly attending to individuals nearby instead of repeatedly moving its head to follow the threat). Responses where young moved were classified as immediately running up to other individuals (within 0.5m) or running independently for shelter. Lastly, responses where young responded independently of other individuals, i.e. not looking or running towards other individuals, were classified as adult-like (same as adults) or non-adult-like (different to adults). We included a total of 323 responses from 48 young (26 females and 22 males; age range: 19 – 180 days) in 19 litters and 10 groups in the analyses.

Playback experiments

Playback stimuli

Playback experiments were conducted to investigate the effect of predator type and urgency level on the reaction time, response duration and time spent vigilant (later referred to as scanning time) following predator type specific alarm calls. Alarm calls used for playback experiments were recorded (sampling frequency 44.1 kHz), within 2 meters from the caller, onto a Sony digital audio tape recorder DAT-TCD D100 (Sony Corporation, Tokyo, Japan) connected to a Sennheiser directional microphone (ME66/K6 with a MZW66 pro windscreen; Old Lyme, CT, U.S.A.). Recordings were digitally transferred to a PC notebook, and call sequences with a high signal to noise ratio were edited using Cool Edit 2000 (Syntrillium, Phoenix, AZ, U.S.A.). We used 6 different alarm-call types and at least 6 different examples of each call type: aerial and terrestrial calls at medium and high urgency level and recruitment calls at low and high urgency level. We only used calls from adults but included calls from both own group members and unfamiliar individuals, as meerkats react similarly to their own and foreign alarms (Manser 1998).

Playback protocol

We conducted playbacks in 11 different groups once young started foraging with the group (28 ± 2.6 days (mean ± SD)) until they reached an age of 95 days. We tested 25 randomly selected female pups and 16 male pups belonging to 23 different litters in a total of 109 playback experiments. Calls were played back with the Sony DAT-TCD D100 recorder connected to a Sony SRS-A60 loudspeaker (frequency response 70–20'000 Hz) and broadcast at amplitudes ranging between 54 – 62 dB, measured 1 m in front of the speaker (Voltcraft 329 Sound Level Meter). These amplitudes correspond to that observed during naturally occurring predator encounters. The duration of each playback varied between 3 – 20 seconds depending on call type (natural call bout duration provided in Manser 2001). We hid the loudspeaker 5 - 10 meters from the pup and started playbacks only if there had not been a natural predator encounter during the previous 20 minutes. Responses were filmed with a Sony digital video camera DCR-PC 120E. To avoid habituation, we conducted a maximum of two playback experiments each day with at least three days passing between successive playbacks in the same group.

Response measures

We analysed the video recordings using frame by frame analysis (12.5 frames/s) in Windows Movie Maker version 5.1 (Microsoft Corporation) and obtained the following measurements for both young and adults: (i) the reaction time (time between onset of call and immediate response), (ii) the response duration (time between onset and end of response). The end of a response was defined as the time when foraging behavior was resumed and (iii) the scanning time. Since the responses of young and adults may not be independent, we only retained those playbacks for which we were able to extract measurements for both. Due to incomplete data on adult measurements, sample size for each variable was therefore reduced. We were able to extract measurements on reaction time from 53 playbacks in 10 groups, response duration from 45 playbacks in 11 groups and scanning time from 30 playbacks in 10 groups.

Predator occurrence

To investigate whether the production, usage and responses to alarm calls may depend on the frequency with which different stimuli are encountered, we extracted, from the long term database, data on natural encounters for the 12 litters followed until sub-adult age (see above). We extracted data for the first three month period following pups' first forage and included a total of 1910 encounters (range 85 – 203 per litter) in the analysis.

Statistical analyses

Statistical analyses were conducted using R for Windows version 2.2.1 (R Development Core Team 2005) and the software packages 'nlme' (Pinheiro et al. 2005) and 'MASS' (Venables & Ripley 2002). Significance level was set at $P < 0.05$ and explanatory terms with a P value above 0.10 were sequentially dropped. All reported tests are two-tailed and analysed with type I SS. We conducted the following analyses:

(i) *Production and usage*: We analysed the proportion of days that different age categories were observed alarm calling (weighted for the time spent observing each group), using the function glmmPQL (penalized quasi-likelihood estimation with binary error structure and logit link function, for details see Breslow & Clayton 1993; Venables & Ripley 2002). We fitted age category as an explanatory term and group identity as a random term.

Remaining proportion data were analysed using the function prop.test (Pearson's chi-squared test statistics). The rate of calling each day was analysed using a one-way ANOVA with the mean number of calls per group and day as a function of age category. To investigate whether the calling rate of young differs depending on the number of adults present, we used a one-way ANOVA with the mean number of calls per individual as a function of the mean number of adults present during the observation period. The age at which different calls are first produced was analysed using a linear mixed effects model procedure fitted with residual maximum likelihood estimation (REML, lme function) (Venables & Ripley 2002). We fitted observation time and call type as explanatory terms and litter identity as a random term. Since assumptions of normality and variance homoscedasticity were violated, we used the natural logarithm of age in this analysis.

(ii) *Vigilance*: The proportion of days spent on raised guard in each age category (weighted for the time observing each group) was analysed using the glmmPQL function with age category fitted as an explanatory term and group identity as a random term. The rate of raised guarding per day was analysed using a one-way ANOVA with the mean number of raised guards per group and day as a function of age category. The number of "guarding away" bouts and mean bout duration per individual was analysed with a linear mixed effects model procedure. We fitted group size and age category as explanatory terms and group identity as a random term. Response variables were square root transformed.

(iii) *Responses*: Due to the sampling procedure of some variables and the unbalanced nature of the data, sample size varies with analyses. We analysed binary response variables using a mixed effects logistic regression model procedure fitted with penalized quasi-likelihood estimation (glmmPQL function, see above). We fitted call type as an explanatory term and individual identity nested within litter and group identity as a random term. Age was also included as an explanatory variable in all models but not discussed here (see Hollén & Manser, in press). To examine whether young cease responding in a non-adult-like fashion and dependent of others (running and looking pooled) to different calls at different ages, we used a linear mixed effects model procedure. Predator type and urgency level eliciting the alarm calls were fitted separately as explanatory terms and group identity as a random term. Age was log transformed in the analysis of dependent responses. To make sure our results were not biased because of highly skewed sample sizes, we ran the same models with more equal sample sizes. Since results did not change, we present the results with original sample sizes.

For playback experiments, we fitted call type (except for scanning time where predator type and urgency level were fitted separately) as an explanatory term and group identity as a random term. We also included adult reaction time, response duration and scanning time to control for dependencies between young and adults within each playback. Response variables were log transformed.

(iv) *Predator occurrence*: The occurrence of different stimuli was analysed using the glmmPQL function with the proportion of encounters (weighted for the total number of encounters per litter) as a function of stimuli type with litter identity as a random term.

Results

Age differences

Alarm-call production

Before 90 days of age, young in only 3 out of the 10 litters were observed to emit alarm calls. Alarm calling increased with age and by the time they reached sub-adulthood, young in all 10 litters were consistently giving alarm calls. However, in all 10 groups there was a difference between age categories both regarding the proportion of days alarm calling ($F_{3,27} = 84.55$, $P < 0.001$), and the rate of calling each day ($F_{3,27} = 25.18$, $P < 0.001$, Fig. 1a). Pups and juveniles called less often and with a lower daily rate than sub-adults, and all young much less than adults. Within the first 12 months, a consistent increase in the rate of alarm calling only began around the age of 220 days (Fig. 1b). Juveniles and sub-adults, however, showed a higher rate of alarm calling each day in groups with fewer adult individuals present ($F_{1,118} = 11.06$, $P = 0.001$).

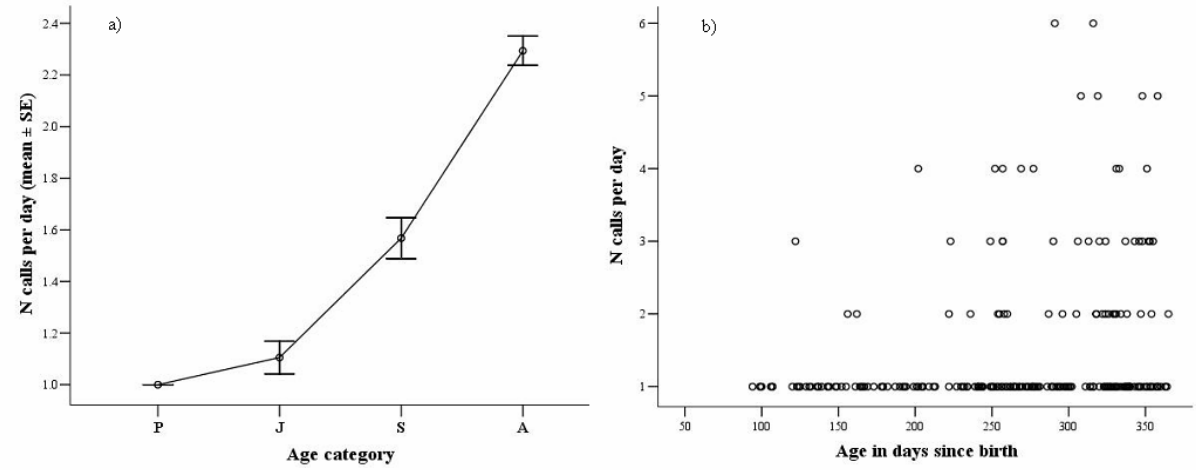

Figure 1. The number of alarm calls given by pups (P), juveniles (J), sub-adults (S) and adults (A) per day (a) and the rate of calling within young (< 12 months) (b). The daily rate of alarm calls was higher in adults compared to pups, juveniles and sub-adults (a) and the increase in calling rate began around 220 days of age (b). Analysis was conducted on mean values per group (N = 10) and age category.

Vigilance

Both the proportion of days observed on raised guard and the number of raised guards per day were lower in young compared to adults (% days: $F_{3,27} = 40.57$, $P < 0.001$; per day: $F_{2,17} = 23.68$, $P < 0.001$, Fig. 2a). Pups less than three months of age were never observed on raised guard and more frequent raised guarding only started after individuals reached six months of age. Young in small groups (< 10 adults), however, were observed on raised guard more often than young in bigger groups ($F_{1,8} = 6.73$, $P = 0.03$). Moreover, those juveniles and sub-adults (N = 41) who were observed to give alarm calls, were also more often on raised guard compared to other young individuals ($F_{1,39} = 8.10$, $P = 0.007$, Fig. 2b).

Similar to raised guarding, young were "guarding away" less often compared to adults. The number of scanning bouts per focal was considerably higher in adults compared to pups, juveniles and sub-adults ($F_{3,53}$ = 7.44, P = 0.003, Fig. 2c). The mean length of each bout was also longer in adults than young ($F_{3,52}$ = 2.99, P = 0.04, Fig. 2d).

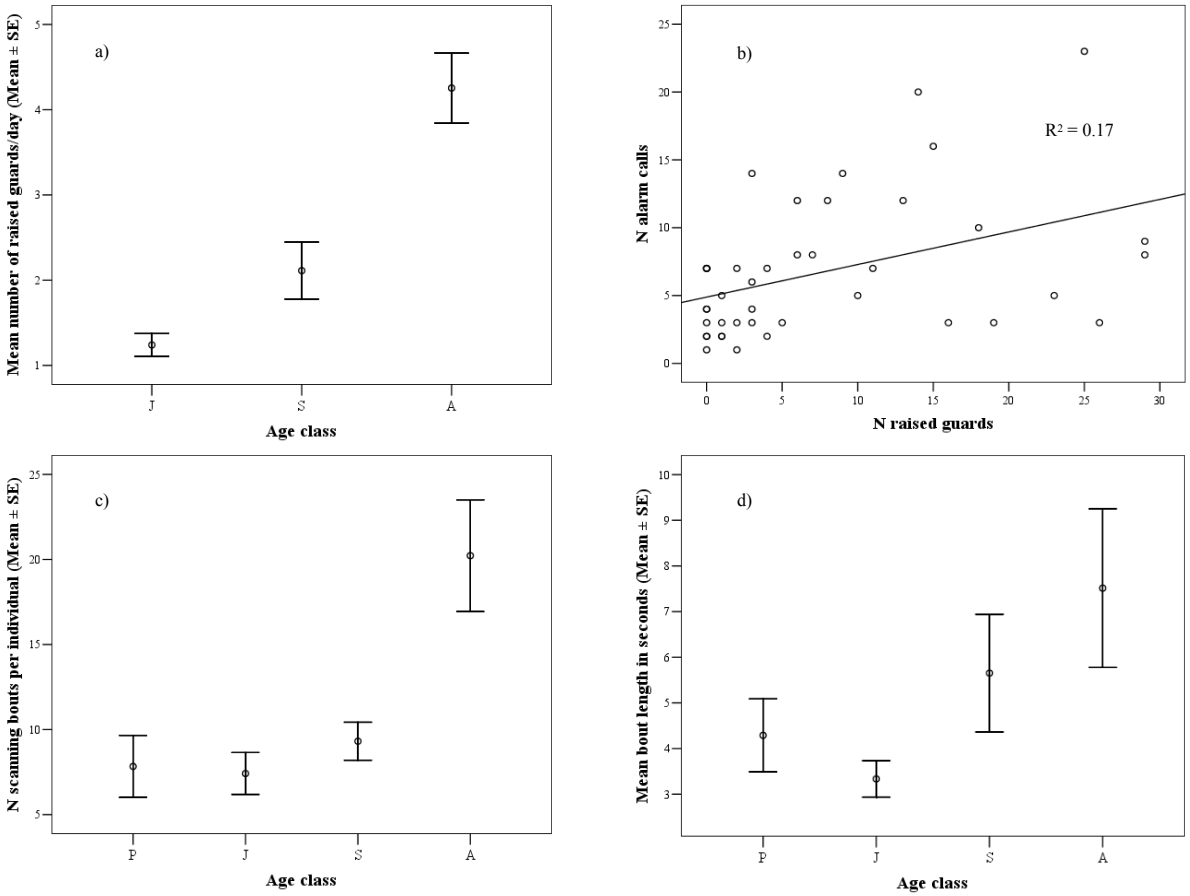

Figure 2. The difference in vigilance behaviour between young and adults. a) the mean number of raised guards per day was lower in juveniles (J) and sub-adults (S) compared to adults (A), b) the number of alarm calls emitted by each young individual during the first year of life increased with increasing number of raised guards by the same individual, c) the number of "guarding away" bouts were higher in adults compared to pups (P), juveniles and sub-adults and d) the mean bout length of each "guarding away" bout increased with increasing age.

Effect of predator type and urgency level

During the first three months following first foraging with the group, young experienced far more aerial than terrestrial or snake encounters ($F_{6,67}$ = 28.67, P < 0.001, Fig. 3). Encounters with birds and bird alarms were also common. Moreover, only 6% of all terrestrial encounters (N=293) were with stimuli posing a real threat compared to 50% of all aerial encounters (N = 646).

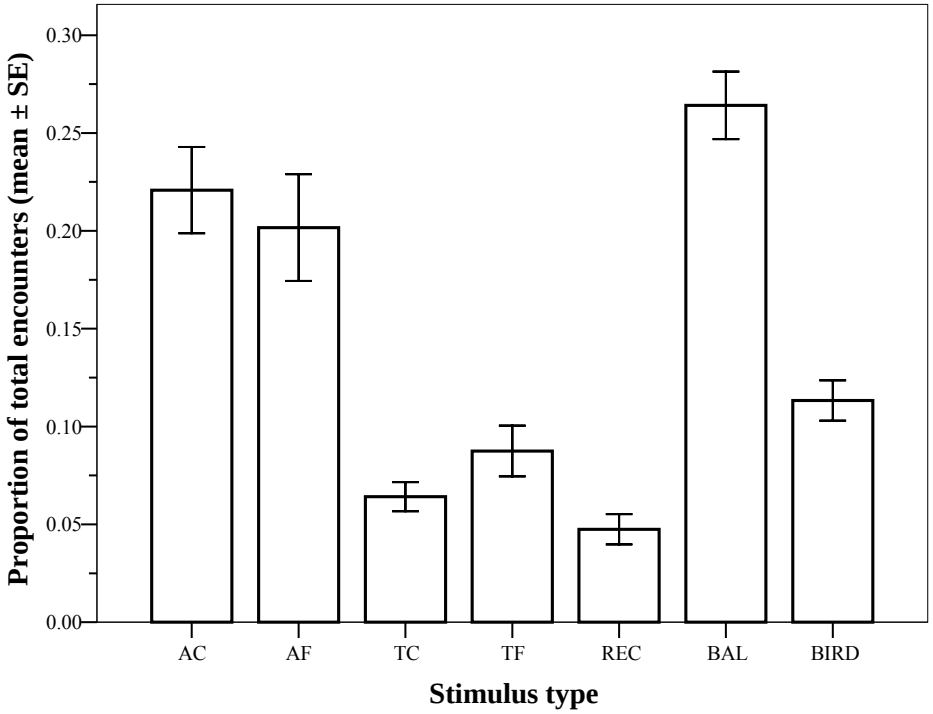

Figure 3. The frequency of occurrence of different stimuli during the first three months after young started foraging with the group. AC = Aerial Closeby, AF = Aerial Far away, TC = Terrestrial Closeby, TF = Terrestrial Far away, REC = Recruitment events, BIRD = non-dangerous birds (excluding vultures), BAL = bird alarm calls. Analysis was conducted on proportion values per litter (N = 12).

Alarm-call production

The age at which alarm calls were first produced by pups and juveniles depended strongly on the type of alarm call ($F_{8,35} = 8.12$, $P < 0.001$). In contrast to adults, in which the majority of alarm calls were predator specific (65%, N = 293), 90% of all alarm calls produced by young were non-predator type specific (N = 293; $\chi^2_1 = 194.7$, $P < 0.001$, Fig. 4). Whereas a maximum of 6 litters out of the 12 (range 0 – 6 litters) gave predator type specific calls during the observed period, 11 of the 12 gave non-predator type specific calls (range 9 – 11 litters). Moreover, non-predator type specific calls were the only calls heard within the first month of emergence. Amongst the predator type specific alarm calls, the aerial low urgency call was the most frequently heard call type (Fig. 4), and was together with recruitment calls emitted earlier than terrestrial calls (median age aerial: 56 days, N = 6 litters; median age recruitment: 61 days, N = 6 litters; median age terrestrial: 85 days, N = 3 litters). Apart from one call emitted by a 4 month old juvenile, aerial high urgency calls were only recorded from young six months or older.

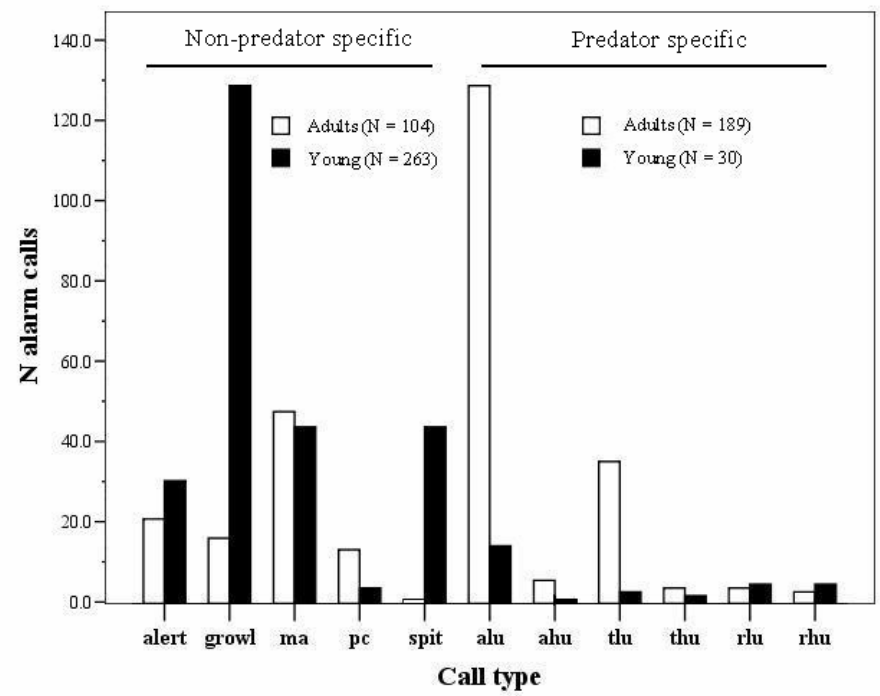

Figure 4. The number of non-predator type specific and predator type specific alarm calls given by young (< 6 months) and adults (> 12 months). Of all alarm calls given by young, 90% were non-predator type specific compared to 35% of those given by adults ($N_{Young} = N_{Adults} = 293$). ma = moving animal alarm call, pc = panic call, alu = aerial low urgency, ahu = aerial high urgency, tlu = terrestrial low urgency, thu = terrestrial high urgency, rlu = recruitment low urgency, rhu = recruitment high urgency.

Correct use

When predator type specific alarm calls were emitted by young, they were emitted in the wrong context more often than that by adults (16 out of 61 and 9 out of 141 cases respectively, $\chi^2_1 = 13.7$, $P < 0.001$, Table 1). However, wrong alarm calls were only elicited in low urgency situations with stimuli far away. Recruitment calls (N = 9) were never emitted in the wrong context but three aerial calls (N = 40) were emitted in response to terrestrial encounters and 4 terrestrial calls (N = 12) in response to aerial encounters. Remaining calls given in the wrong context were aerial calls emitted in response to non-threatening birds (Table 1). Although adults occasionally emitted aerial calls in response to birds, they did so less often than young (7 out of 141 and 9 out of 61 cases respectively; $\chi^2_1 = 7.89$, $P = 0.005$).

Table 1. The number of terrestrial, aerial, recruitment and non-predator type specific alarm calls given by meerkats in different age categories to different types of stimuli. The unk ID represents cases where the identity of the calling individual could not be established.

	Terrestrial species	**Aerial species***	**Birds**	**Snakes/ Scents**	**N ind**
Adults (>2 years)					
Terrestrial calls	14	0	0	0	
Aerial calls	0	39	4	0	10 ♀♀
Recruitment calls	0	0	0	3	20 ♂♂
Non-specific calls	19	8	2	0	
Adults (1-2 years)					
Terrestrial calls	11	2	0	0	
Aerial calls	0	63	3	0	32 ♀♀
Recruitment calls	0	0	0	2	15 ♂♂
Non-specific calls	19	20	5	0	
Juveniles + Sub-adults (90 - 365 days)					
Terrestrial calls	7	2	0	0	
Aerial calls	0	12	4	0	21 ♀♀
Recruitment calls	0	0	0	5	10 ♂♂
Non-specific calls	10	11	7	2	7 unk ID
Pups (< 90 days)					
Terrestrial calls	1	2	0	0	
Aerial calls	3	16	5	0	19 ♀♀
Recruitment calls	0	0	0	4	22 ♂♂
Non-specific calls	24	22	38	2	45 unk ID

* Including raptors and vultures but no other bird species

Alarm-call responses

The type of alarm call emitted did not influence the probability of young initially responding like adults ($F_{5,194} = 0.81$, $P = 0.54$), or scanning their surroundings instead of looking towards other individuals ($F_{5,100} = 1.21$, $P = 0.31$), but did influence whether young ran to other individuals or not ($F_{5,122} = 2.87$, $P = 0.02$). However, this was only because young were more likely to run independently than run to others in response to bird alarm calls compared to any other conspecific call type. Young stopped showing non-adult-like responses earlier in response to calls elicited in high urgency situations compared to low urgency situations ($F_{1,27} = 4.69$, $P = 0.04$), whereas there was no difference between predator types ($F_{1,27} = 1.08$, $P = 0.31$, Fig. 5a). In contrast, the age at which young stopped responding dependently of others was influenced by both urgency level ($F_{1,53} = 3.73$, $P = 0.06$) and predator type ($F_{1,53} = 15.76$, $P < 0.001$, Fig. 5b). Young stopped running to others later in response to low urgency than high

urgency calls as well as aerial compared to terrestrial calls. The difference between aerial and terrestrial calls was most pronounced in low urgency situations.

Playback experiments showed that, in contrast to adults, the type of call played back affected the response duration of young (adults: $F_{5,29} = 0.42$, $P = 0.83$; young: $F_{5,26} = 3.00$, $P = 0.03$). However, this difference is only due to young staying alert longer in response to terrestrial high urgency calls compared to any other call type. Alarm-call type did not influence how fast young reacted ($F_{5,36} = 1.56$, $P = 0.20$), or the amount of time spent scanning the surroundings afterwards (predator type: $F_{2,15} = 1.48$, $P = 0.26$; urgency level: $F_{1,15} = 0.04$, $P = 0.85$).

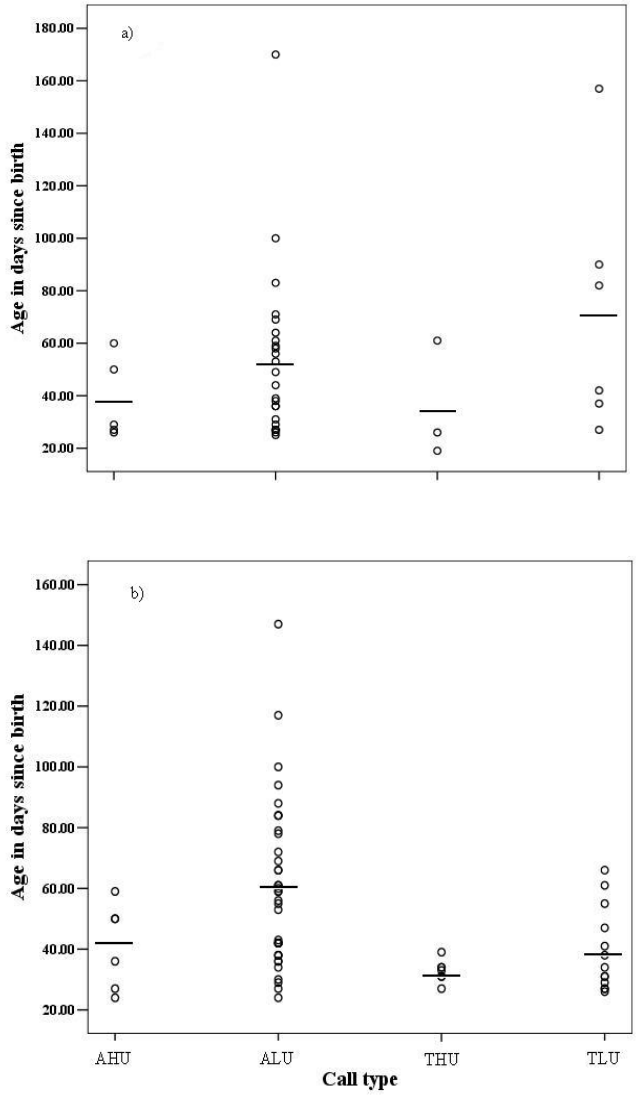

Figure 5. Responses to naturally occurring alarm calls (AHU = aerial high urgency, ALU = aerial low urgency, THU = terrestrial high urgency, TLU = terrestrial low urgency) showing: a) the age at which young stopped showing non-adult-like responses ($N_{AHU} = 5$ ($N_{tot\ adult\text{-}like\ +\ non\text{-}adult\text{-}like} = 20$); $N_{ALU} = 24$ ($N_{tot\ adult\text{-}like\ +\ non\text{-}adult\text{-}like} = 75$); $N_{THU} = 3$ ($N_{tot\ adult\text{-}like\ +\ non\text{-}adult\text{-}like} = 12$); $N_{TLU} = 6$ ($N_{tot\ adult\text{-}like\ +\ non\text{-}adult\text{-}like} = 18$)) and b) the age (back transformed) at which young stopped running to and looking towards other individuals (dependent responses) ($N_{AHU} = 6$ ($N_{tot\ dependent\ +\ independent} = 18$); $N_{ALU} = 39$ ($N_{tot\ dependent\ +\ independent} = 95$); $N_{THU} = 7$ ($N_{tot\ dependent\ +\ independent} = 16$); $N_{TLU} = 13$ ($N_{tot\ dependent\ +\ independent} = 25$)). Horizontal lines represent mean values.

Discussion

Young meerkats, especially before six months of age, were the least likely individuals to give alarm calls. Our results are similar to those obtained for infant vervet monkeys (Seyfarth & Cheney 1980) and suggest that experience may play an important role in alarm-call production. However, consistent with findings in many juvenile mammals (see Arenz & Leger 2000), young meerkats were much less vigilant compared to adults. Assuming that predator detection depends on scan duration and scan frequency (McNamara & Houston 1992), more alert individuals would be more likely to detect predators and presumably more likely to emit alarm calls. Indeed, adult meerkats guarding from a raised position have been shown to emit alarm calls more frequently compared to foraging group members (Manser 1998). Similarly, calling amongst young increased when on raised guard. As do adult group members (Clutton-Brock et al. 1999b), young also increased their guarding with decreasing group size. Since we concurrently found a higher calling rate amongst young in groups with few adults present, our results suggest that not only age but also vigilance play a role in determining alarm calling behaviour.

We also found a clear age difference in when different call types were produced by young. Non-predator type specific calls were produced much earlier compared to predator type specific calls. If referential alarm calls evolve from motivational signals as proposed by Macedonia (1993), it may make sense that predator type specific calls require more learning than others and appear later in the repertoire. Moreover, the speed of learning may depend on the frequency with which different call types are heard (see Hauser 1988; Mateo 1996b). Aerial encounters occurred more frequently than terrestrial or snake encounters and aerial low urgency calls were most common amongst the predator type specific calls produced by young. However, aerial high urgency alarm calls which were emitted rather frequently by adults, were only recorded from young four months or older. Also, we have no support for auditory experience to play a role in any developmental modification of alarm-call structure (LI Hollén & MB Manser, unpublished data). Thus, the precise role of auditory experience has still to be systematically determined.

Young meerkats occasionally gave alarm calls in the wrong context, suggesting that young may need experience to restrict alarm calling to predators belonging to particular classes (see also Seyfarth & Cheney 1980). It is also possible that incorrect calling reflects a higher vulnerability amongst young (Cheney & Seyfarth 1981). However, since young more often than adults also gave alarm calls to stimuli posing no threat to them, such as birds, differences between young and adults can not be explained only in terms of vulnerability differences. That birds were usually encountered at very close distances and wrong alarm calls to actual predators only given when predators were far away, suggests that mistakes may be affected by the distance to the stimuli. Distance might affect their judgement either because anything moving very closeby is worthwhile alarming at or because of identification problems at long range (Seyfarth & Cheney 1986).

The correct use of recruitment alarm calls given in response to snakes or deposits seemed to develop earlier than that of aerial or terrestrial calls. Since recruitment calls function to recruit others to a threat too dangerous to mob alone (Manser 2001), it may be more crucial to give contextually appropriate calls early on. Supporting this result, we subsequently found that when exposed to predatory secondary cues, young individuals emitted the appropriate recruitment calls at a relatively early age and that these calls underwent less structural modification during development compared to aerial or terrestrial calls (LI Hollén & MB Manser, unpublished data). A quick acquisition of predator recognition through chemical alarm cues has been shown in a variety of aquatic prey (Chivers & Smith 1998) and being able to show correct anti-predator behaviour without direct contact with predators could have serious advantages for prey species.

Young meerkats seem able to discriminate and respond to graded variations in urgency within a call type (see also Fischer et al. 2000). Young stopped showing non-adult-like responses at an earlier age in response to high urgency than low urgency alarm calls. Although reaction time and scanning time were not affected by the type of call played back, young also stayed alert longer following playback of terrestrial high urgency compared to low urgency calls. Similarly, young stopped relying on other group members later in low urgency than in high urgency situations. Selection may have favoured early correct and independent responses to alarm calls signalling high urgency due to a greater risk of being predated with predators closeby (see also Mateo 1996a). In contrast, responding correctly to alarm calls does not seem to be contingent upon the particular predator approaching. However, young were older when they stopped relying on others in response to aerial compared to terrestrial stimuli. As aerial predators are faster moving and constitute a greater risk than herbivores, to which most terrestrial alarms were given, young may be safer by relying on others. In situations involving an immediate threat, however, a quick escape to shelter may be crucial irrespective of predator type, possibly explaining why the difference between aerial and terrestrial stimuli was much smaller in high urgency situations.

To conclude, our results suggest that meerkat young, like other young animals (e.g. vervet monkeys: Seyfarth et al 1980; Belding's ground squirrels: Mateo 1996b) and children (Madole 1999), are capable of early object classification. Despite that, however, both the meerkats' use of alarm calls and responses to them must develop over the first year of life. Experience combined with an increase in alertness may play an important role. Moreover, this development is to some extent, although not greatly, sensitive to the threat posed by different situations. Rather than the actual type of stimuli approaching, the level of response urgency measured as the distance to stimuli seems to be most influential. Given the obvious benefits, development of anti-predator behaviour adapted to the threat posed by different predators may be common, with similar developmental trajectories expected in species facing similar risks.

Acknowledgements

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CHAPTER 4

Motivation before meaning: motivational information encoded in meerkat alarm calls develops earlier than referential information

In press in The American Naturalist

Motivation before meaning: motivational information encoded in meerkat alarm calls develops earlier than referential information

Linda I. Hollén[1] and Marta B. Manser[1]

[1] Verhaltensbiologie, Zoologisches Institut, Universität Zürich, Winterthurerstrasse 190, 8057 Zürich, Switzerland

Abstract

In contrast to historical assumptions about the affective nature of animal vocalizations, it is now clear that many vertebrates are capable of producing specific alarm calls in response to different predators, calls which provide information that goes beyond the motivational state of a caller. However, although these calls function referentially, it does not mean that they are devoid of motivational content. Studies on meerkats (*Suricata suricatta*) directly support this conclusion. The acoustic structure of their alarm calls simultaneously encodes information that is both motivational (level of urgency) and referential (predator-specific). In this study, we investigated whether alarm calls of young meerkats undergo developmental modification, and whether the motivational or the referential aspect of calls changes more over time. We found that, based on their acoustic structure, calls of young showed a high correct assignment to low and high urgency contexts, but in contrast to adults, low assignment to specific predator types. However, the discrimination among predator types was better in high urgency than low urgency contexts. Our results suggest that acoustic features related to level of urgency are expressed earlier than those related to predator-specific information, and may support the idea that referential calls evolve from motivational signals.

Introduction

Animal signals have historically been thought to lack the capacity to function referentially, that is, providing listeners with information about external objects or events, one of the key characteristics of human speech. Instead, vocalizations of animals have been seen as mainly reflecting the caller's motivational state (reviewed in Marler et al. 1992; Seyfarth & Cheney 2003). Studies over the past 20 years have created a more complicated picture, acknowledging the fact that animal signals, as human speech, can encode specific information linked to external stimuli which goes beyond the motivational state of a signaller (see Seyfarth & Cheney 2003). Nevertheless, no animal or human signal that has been identified as referential is devoid of motivational content, although the proportional contributions of each component may vary widely within and between species (e.g. Marler 1977; Marler et al. 1992; Macedonia & Evans 1993; Bachorowski & Owren 1995; Seyfarth & Cheney 2003). The same vocalization therefore has the potential to convey information both about an external referent and about the caller's level of emotion. Recent research has also led to a general agreement that 'motivation' and 'reference' are logically distinct and independent dimensions. Even if animal signals are pure expressions of the callers' emotions, as long as they are elicited by specific stimuli, they can convey referential information to listeners (reviewed in Seyfarth & Cheney 2003).

Alarm calls are particularly well suited to address questions regarding the relative role of referentiality and motivation in animal signals (Macedonia & Evans 1993; Evans 1997; Blumstein 2002). Many species of nonhuman primates (reviewed in Macedonia & Evans 1993; Zuberbühler 2000, 2001), and also chickens (*Gallus gallus domesticus*) (Evans et al. 1993), give acoustically distinct alarm calls in response to different types of predators, whereas alarm calls of other species such as ground squirrels (*Spermophilus sp.*) and marmots (*Marmota sp.*), lack the high degree of referential specificity and reflect differences in response urgency perceived by the caller (reviewed in Macedonia & Evans 1993). However, it is likely that together with contextual cues, the alarm calls of ground-dwelling sciurids may provide listeners with probabilistic identification of predator types. Similarly, the production specificity of nonhuman primate alarm calls varies, suggesting that variation in motivational state of a caller plays an important role in the production of the specific calls (Macedonia & Evans 1993). Thus, it seems likely that vocal signals in a wide array of species have both referential and motivational characteristics, as has been shown in human speech (e.g. Bachorowski 1995). Recent work on the alarm calls of meerkats (*Suricata suricatta*) directly supports this conclusion and clearly demonstrates the entwined role of motivation and reference in animal communication (Manser 2001; Manser et al. 2002).

While animal vocalizations can be both motivational and referential in the information they convey, we know little about how the characteristics encoding such information develop. Children seem to enter the language system of word use through the use of vocal forms which are more adult-like in sound than in their semantic function, and may stimulate participation in social interactions rather than transmitting information (Locke & Snow 1997). To our knowledge, no study on nonhuman vocal production has investigated whether, like in children, referential aspects of calls develop later than other aspects. Since we know the role of motivation and reference in meerkat alarm calls, and the acoustic features encoding this information, meerkats provide a good opportunity to investigate how these two different attributes of calls develop.

Meerkats are small cooperatively breeding mongooses inhabiting the arid regions of Southern Africa (Clutton-Brock et al. 1999a). They are preyed upon by several raptors, mammalian predators, and snakes (Clutton-Brock et al. 1999b), which elicit acoustically distinct alarm calls (Manser 2001). Additionally, within each call class, the acoustic structure of calls varies depending on the distance to the predator. Calls given in response to predators

closeby (termed “high urgency”) are acoustically different from those given in response to the same predator encountered at a far distance (termed “low urgency”). Listeners thus acquire information about specific predators and the level of danger they represent, allowing them to respond appropriately in specific contexts (Manser et al. 2001). The acoustic parameters accounting for variation among predator types are different from those explaining the variation across the levels of urgency (Manser 2001). Moreover, while changes in acoustic structure along the dimension of urgency are consistent across different predator types, with calls becoming harsher and noisier as urgency increases, the referential information about each predator type is not encoded in any consistent way. The features of meerkat alarm calls might therefore support the idea that referential alarm calls evolve from motivational calls in the repertoire (Macedonia 1993). Supporting this, we previously found that although young less than six months of age rarely uttered alarm calls, calls that seem to reflect intense fear were present already on the first day of emergence, whereas calls specific to particular predator types appeared much later in the repertoire (L. I. Hollén and M. B. Manser, unpublished data).

In this study, we investigated whether the acoustic aspects of calls related to referential information also undergo more developmental modification than motivational aspects. Specifically we asked whether: (i) the calls of young, as those of adults, can be classified correctly according to the context in which they are given based on their acoustic structure, (ii) the discrimination along the level of urgency differs from the discrimination along predator types, (iii) the change in acoustic structure along the dimension of level of urgency is consistent across predator types, (iv) the acoustic parameters explaining differences between adult calls can be used to correctly assign the calls of young and vice versa. Finally, we examined which acoustic parameters are important in determining variance amongst individuals of different ages.

Methods

Study site and animals

We studied the ontogeny of alarm-call production in 13 groups of free ranging but habituated (close observation <1 m) meerkats near VanZyl’s Rus in the South African part of the Kalahari Desert (26º58´S, 21º49´E) (details of study site provided in Clutton-Brock et al. 1999b) from January to July 2003 and from October 2003 to June 2004. All animals were marked for individual identification with hair dye or hair cuts applied to their fur non-invasively during sunning at the morning sleeping burrow. All individuals had been monitored since birth and their exact ages were therefore known.

Recording methods and call selection

We analysed calls obtained from recordings during natural predator encounters, and from a manipulation experiment (see below). Alarm calls obtained during natural encounters were recorded from pups (less than 3 months old), juveniles (3-6 months old), sub-adults (6-12 months old), and adults (more than 12 months old). Pups from 12 litters were followed regularly (on average once per week) from their emergence (mean ± SD: 17 ± 2.4 days) until reaching sub-adult age. Calls from other pups, juveniles, sub-adults and adults were recorded ad libitum whenever visiting a group. We also conducted a manipulation experiment in order to test the development of recruitment alarm calls under controlled conditions. Recruitment calls are emitted in response to snakes and deposits such as faecal, urine or hair samples of other meerkats or predators, and collectively termed recruitment calls since they function to

recruit other group members to investigate or mob the threat (Manser 2001). We presented the meerkats with hair samples of an African wildcat (*Felis lybica*), which has been shown to reliably elicit recruitment alarm calls in adults (Graw 2005). The hair, prior to the experiment cut from a salt treated skin (obtained from a road kill carcass stored in a freezer), was placed in front of a foraging individual. Young (< 6 months) were exposed to the hair at four different stages during development (age in days (mean ± SD): stage 1: 41 ± 6, stage 2: 78 ± 7, period 3: 114 ± 6, period 4: 161 ± 17), and after each presentation, adult individuals were also tested. We tested a total of 69 young individuals (37 females and 32 males), and 43 adult individuals (18 females and 27 males) in 12 groups.

Alarm calls were recorded at a distance of 1-2 m from the caller, at 44.1 kHz sampling frequency, using a Sennheiser directional microphone (ME66/K6 with a MZW66 pro windscreen; frequency response 40–20000 Hz ± 2.5 dB, Old Lyme, CT, U.S.A.) connected to a Sony digital audio tape recorder DAT-TCD D100 (frequency response: 20–20000 Hz ± 1 dB, Sony Corporation, Tokyo, Japan) or a Marantz PMD-670 solid state recorder (D&M Holding, Inc., Kanagawa, Japan). Type and distance to stimuli (naturally occurring) eliciting the calls were spoken onto the tape. Calls were uploaded on to a PC (sampling frequency: 44.1 kHz; resolution: 16 bit), and visually inspected using Cool Edit 2000 (Syntrillium, Phoenix, AZ, U.S.A.). Only those calls with sufficiently high quality were chosen for analysis.

We examined five predator-specific call types: aerial, terrestrial and recruitment calls at low urgency level, and aerial and recruitment calls at high urgency level (for spectrograms, see figure 1). Terrestrial high urgency calls were excluded due to low sample size for young individuals. In brief, aerial and terrestrial calls are given in response to aerial and mammalian stimuli, causing meerkats to scan their surroundings or move to a bolthole (Manser 2001; Manser et al. 2001). Predators at a far distance (aerial: > 200 m, terrestrial: > 50 m) typically elicit low urgency calls whereas predators closeby (aerial: < 200 m, terrestrial: < 50 m) elicit high urgency calls. Recruitment high urgency calls are emitted in response to both snakes and deposits, whereas recruitment low urgency calls are mainly given when encountering deposits (Manser 2001). We also included one call type, the growl call, which is not specifically related to a single predator type. These calls are often heard from young when non-dangerous stimuli such as birds make sudden movements within a few meters of the caller. Because these calls sound similar to other predator-specific high urgency calls, we included them to see whether they are similar based on their acoustic structure.

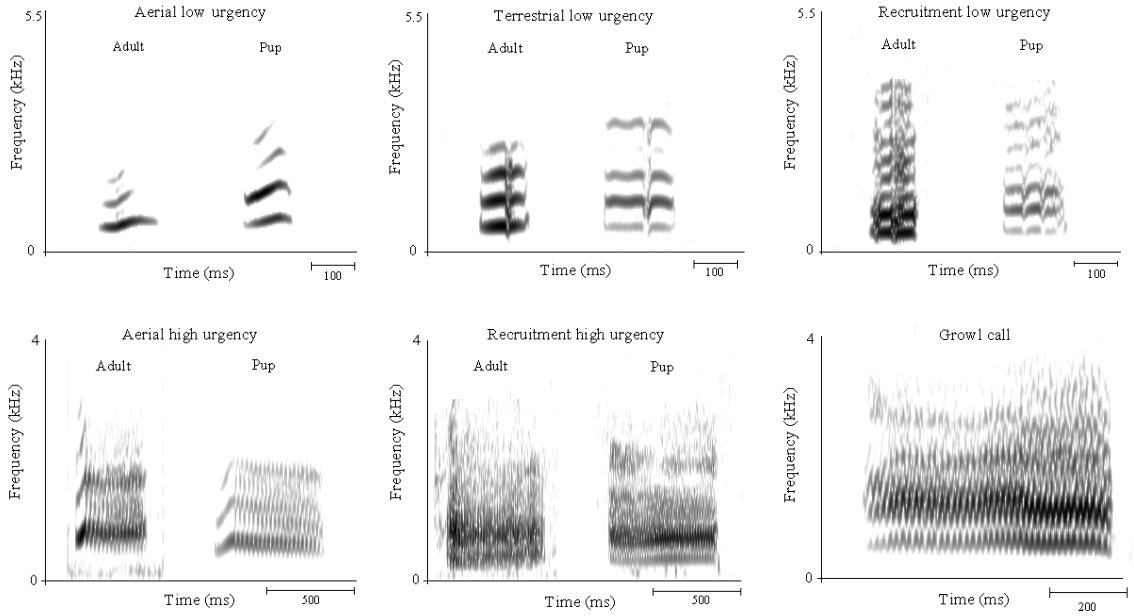

Figure 1. Spectrograms of the five different predator type specific alarm calls and the one non-predator specific call (growl call, uttered by pups only) included in the analyses. Calls are exemplars from adults older than 1.5 year and young individuals 4 months or less.

Acoustic analysis

We first conducted a fast Fourier transformation (1024-point FFT; Hamming window; time step: 1.45 ms; overlap: 98.43%; frequency range: 11.025 kHz; frequency resolution: 28 Hz) of all calls using AVISOFT-SASLab pro 4.38 (R. Specht, Berlin, Germany). The resulting frequency – time spectra were analysed with LMA 2005 (developed by K. Hammerschmidt), a software tool that extracts a large number of call parameters from acoustic signals (for detailed description of the algorithms and calculation of parameters, see Schrader & Hammerschmidt 1997). A list of the parameters used in our analyses is given in appendix A.

We first calculated a set of parameters, including start, minimum, maximum, and median frequency of the first two dominant frequency bands. The dominant frequency bands are characterized by amplitudes that exceed given thresholds in a consecutive number of cells. In tonal calls, these bands represent the fundamental frequency and its harmonics whereas in atonal signals, the dominant frequency peaks reflect the frequencies with the highest energy. Secondly, we determined the statistical distribution of spectral energy measured as the first and second quartiles of the distribution of frequency amplitudes in the spectrum. Thirdly, we calculated the local and global modulation of the first dominant frequency band. Fourthly, we determined the location and the modulation of the peak frequency (the frequency with the highest amplitude in a time segment). Fifth, we measured temporal parameters such as call duration, and temporal location of minimum and maximum frequencies. Finally, we also determined the mean and maximum harmonic-to-noise ratio. Including many acoustic parameters allows for a comprehensive analysis of complex patterns without any a priori assumptions about the importance of specific parameters (see Schrader & Hammerschmidt 1997), and can also improve the rate of correct assignment (Hammerschmidt & Todt 1995).

Statistical analyses

We conducted all analyses in R for Microsoft Windows version 2.2.1 (R Development Core Team 2005) using the software packages 'MASS' (Venables & Ripley 2002), 'Hmisc' (Harrell et al. 2006), 'Design' (Harrell et al. 2005) , and 'ipred' (Peters & Hothorn 2004). Since certain parameters measured for some call types could not be reliably estimated for other call types, the number of parameters included in the analyses varies (table 1). Sample sizes for young and adults also vary depending on call type (table 1). Assumptions of multi – and univariate normality and homogeneity of variances were fulfilled.

We used a discriminant function analysis (DFA) method (function lda in 'MASS') to determine the classification probabilities of alarm calls uttered by young (< 12 months) and adults (> 12 months). DFA identifies linear combinations of predictor variables that best characterize the differences among groups, and combine the variables into one or more discriminant functions depending on the number of groups to be classified (N functions = N groups -1). This analysis method provides a classification procedure that assigns each call to its appropriate group (correct assignment) or to another group (incorrect assignment). For external validation, we used a 10-fold cross validation technique (function errorest in 'ipred'). The data is randomized and partitioned into 10 folds (sets) of approximately equal size. In each of 10 turns, 9 of the folds are then used for establishing the model (training data) and the remaining 1 fold for estimating the model's validity (test data). Different folds are used as training and test data in each turn. To calculate assignment probabilities expected by chance, we used a bootstrap approach (n repeats = 1000). While taking into account the initial sample sizes in the actual data, random numbers were assigned to each call class. Chance probabilities are presented with the mean of all repeats ± 1 SE. Because of questions about the use of unbalanced designs in DFA, we also conducted analyses with balanced sample sizes (randomly drawn cases) to verify that our results were not biased. Since this was not the case, we report the results with the original sample sizes. Moreover, the DFA was set to work on the prior probabilities of each class, which were calculated from the initial sample sizes.

To avoid correlated predictor variables in the DFA, we first conducted principal component analyses (PCA) (function princomp in 'MASS'), which creates a new set of uncorrelated variables, each of which is a linear combination of the original variables. Since the PCA needs a complete correlation matrix, we first replaced missing values among our acoustic parameters using a multiple imputation (n = 20) approach (function aregImpute in 'Hmisc', Little 2004). Components (unrotated) with eigenvalues greater than 1 were retained (> 70% of the original variance explained), and used as classifiers in the DFA. To test whether the components explaining differences between adult calls can be used to assign the calls of young and vice versa, we first conducted separate PCA on adults and young. The components extracted from adults calls were then used as training data for the calls of young and vice versa. Finally, to test whether the change in acoustic structure along the dimension of level of urgency is consistent across predator types, we took those components explaining the difference between the high and low levels of urgency for aerial calls and investigated whether these components could also explain the high and low levels of urgency for recruitment calls. We then did the reverse and investigated whether the components for recruitment calls could explain the high and low levels of urgency for aerial calls.

To test for univariate differences in acoustic structure of calls between individuals of different ages, we conducted a set of general linear models (function lm in 'MASS'). For each call type, we first conducted a PCA and then used the unrotated principal components as response variables in the models (loadings of acoustic parameters on each component are provided in appendix B). The number of components and the amount of variation explained by these components is displayed in table 1. Since we were sometimes not able to determine the identity of the calling individual, we pooled individuals < 12 months (young) and those >

12 months (adults) and fitted age as a categorical term for all call types except aerial low urgency calls, for which we were able to fit age as a continuous (linear and quadratic) term. For aerial low urgency calls we also fitted, before age, factors (true or false) coding for whether individuals were younger than 3 months, younger than 6 months, or younger than 12 months. In this way, we could examine in more detail where changes during development may occur. Sex was included as an explanatory term in all models. All tests were 2-tailed and significance level set at $P < 0.05$. Terms with P values above 0.10 were removed from the models.

Table 1. Sample sizes for the different call types included in the uni- and multivariate analyses (growl call not included in the univariate analysis). N parameters = the number of acoustic parameters from which principal components were extracted (numbers included in PCA preceding DFA represented in brackets), n pc = the number of principal components included in further analyses (multivariate analyses in brackets), variance % = the % of the original variance explained by the principal components in the univariate analyses (for multivariate: > 70% for all). Alu = Aerial low urgency, Tlu = Terrestrial low urgency, Rlu = Recruitment low urgency, Ahu = Aerial high urgency, Rhu = Recruitment high urgency.

call type	n adults	n young	n parameters	n pc	variance %
Alu	61	38	27 (16)	5 (5)	72
Tlu	15	9	24 (16)	5 (5)	80
Rlu	13	12	23 (16)	5 (5)	78
Ahu	13	6	13 (13)	4 (3)	81
Rhu	20	9	13 (13)	4 (3)	77
Growl	-	18	13 (13)	(3)	

Results

Level of urgency discrimination

For both adults and young, calls could statistically be accurately distinguished on the basis of urgency level. Adult calls (aerial and recruitment calls pooled) showed a 96% correct assignment into high and low urgency contexts before cross validation, and 93% afterwards (figure 2). Similarly, the calls of young showed a high 92% correct assignment before and after cross validation (figure 2). For both adults and young, this is much higher than the mean of 52 ± 0.03% expected by chance. Moreover, young tested on the calls of adults and vice versa yielded a high correct assignment of 81% and 90% respectively. When we analysed aerial and recruitment calls separately, we also obtained high correct assignment probabilities (> 85% for both young and adults). The analyses conducted to test whether the change in acoustic structure along the dimension of level of urgency is consistent across predator types yielded a mean correct assignment of 87 ± 0.8% for young, and 80.1 ± 1.4% for adults, which is higher than that expected by chance (50 ± 0.07%). Assignment probabilities equal to or greater than that obtained in all analyses were generated by chance in less than 3% (adults = 0.8%, young = 2.4%) of all bootstrap repeats (n = 1000).

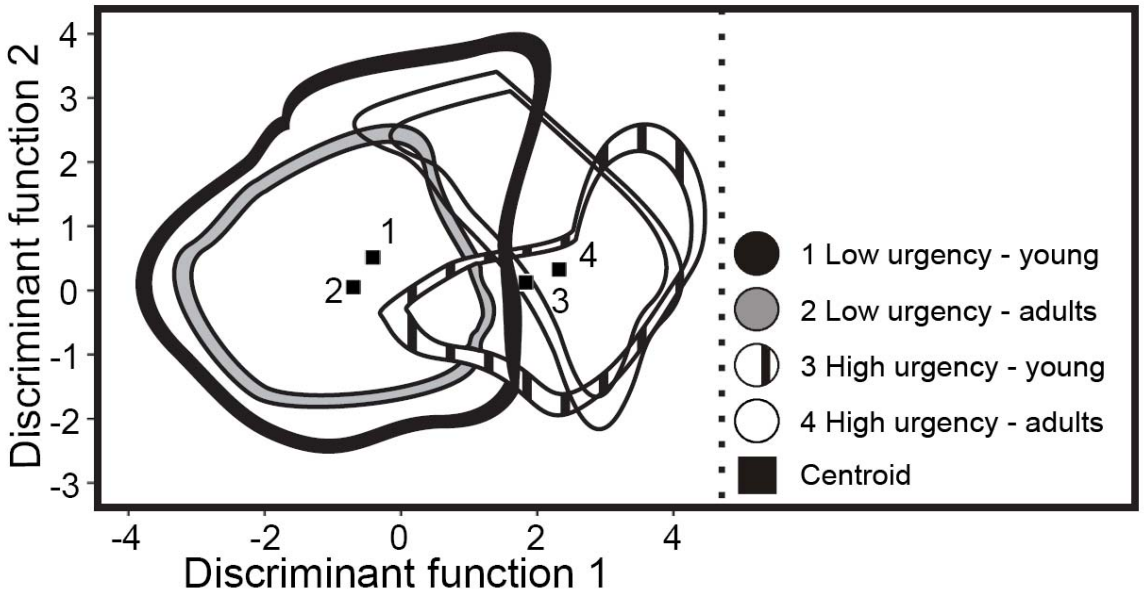

Figure 2. The discrimination between calls uttered in low and high urgency contexts for adults and young. The outer lines represent contour lines around all data points classified to each call type.

Predator type discrimination

Although the calls of adults were well distinguished between predator types, calls of young showed more overlap. For calls emitted in low urgency contexts, the DFA yielded two discriminant functions with the first function accounting for 79% of the variance in adult calls and 86% in young. The calls of adults showed a correct assignment of 86% before and after cross validation compared to 42 ± 0.02% expected by chance (figure 3 *A*) (for parameters distinguishing between call types in adults, see Manser 2001). The calls of young yielded a correct assignment of 85% but this decreased to only 63% after cross validation (41 ± 0.03% expected by chance) (figure 3 *B*). Although greater than that expected by chance, values equal to or greater than 63% were obtained in 16% of all bootstrap repeats. In contrast, only 3% of the repeats for adults calls yielded values ≥ 86% by chance. Moreover, when the calls of young were tested with the principal components extracted from adult calls, they showed a correct assignment of only 46%, thus similar to that expected by chance. Similarly, if the calls of adults were tested on the calls of young, adult call assignment was reduced to 55%.

For both adults and young, the discrimination of predator types was better in high urgency contexts than low urgency contexts. For calls emitted in high urgent contexts, the DFA on adult calls yielded before and after cross validation a high correct assignment of 97% and 94% respectively (figure 3 *C*). The calls of young showed a correct assignment of 80% before and 73% after validation (figure 3 *D*). For both adults and young, this is higher than the mean of 50 ± 0.05% expected by chance. Values equal to or greater than 73% were, however, obtained in 21% of all bootstrap repeats (3% of the cases for adults yielded values ≥ 94%). Still, when used as a test set on the adult training set, the calls of young were classified with a high correct assignment of 80%. For adults, the correct assignment stayed the same (94%) when tested on the calls of young. The second analysis including the non-specific growl call yielded a correct assignment of 73 % before and 70% after cross validation compared to 38 ± 0.03% expected by chance. This showed that growl calls clustered relatively separately from the other high urgency call types.

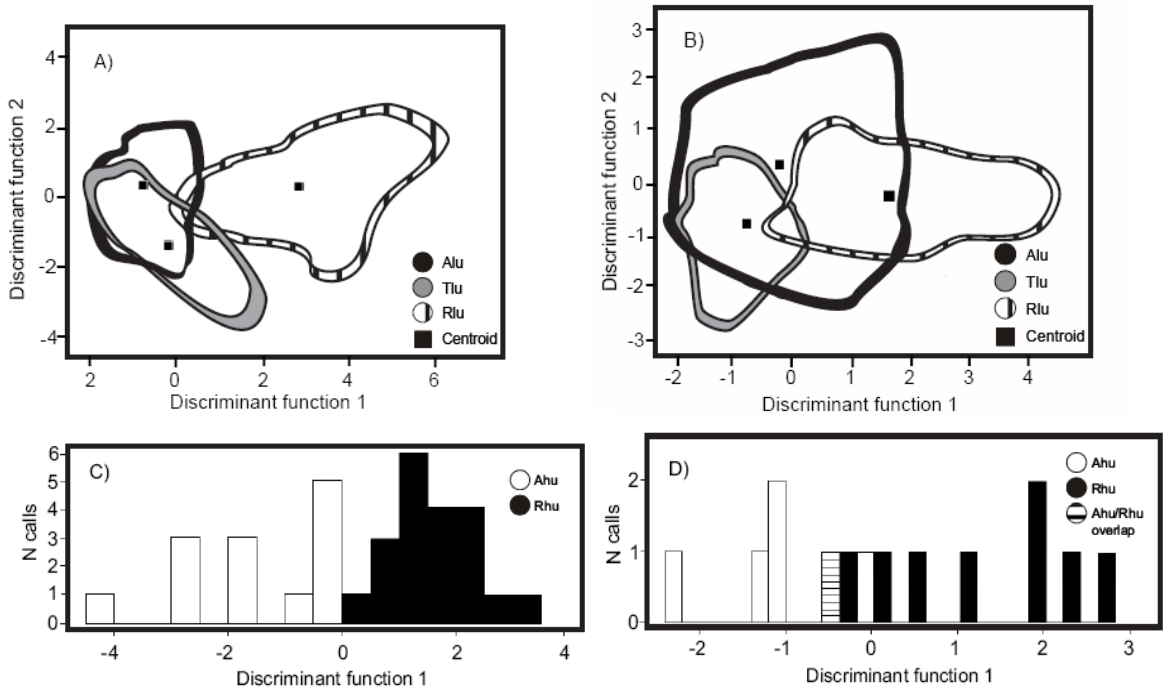

Figure 3. Classification results from the discriminant function analyses on predator-specific alarm calls emitted in low (*A*, *B*) and high (*C*, *D*) urgency contexts by adults (*A*, *C*) and young (*B*, *D*). Alu = Aerial low urgency, Tlu = Terrestrial low urgency, Rlu = Recruitment low urgency, Ahu = Aerial high urgency, Rhu = Recruitment high urgency. The outer lines in A and B represent contour lines around all data points classified to each call type.

Age differences in call structure

When we tested the univariate differences for those acoustic parameters reliably estimated for each call type in low urgency contexts, aerial, terrestrial, and recruitment calls, all showed some modification with age (table 2). For all three call types, there was a difference in the scores of the first principal component between individuals of different ages (aerial: $F_{1,92}$ = 6.63, P = 0.01; terrestrial: $F_{1,22}$ = 4.46, P = 0.046; recruitment: $F_{1,18}$ = 9.09, P = 0.007). For aerial and recruitment calls, the acoustic parameters highly associated with this component were parameters describing the peak frequency and the first and second dominant frequency band with higher values in young than adults. However, for aerial calls, a significant interaction between individuals younger than three months and the remaining ages showed that some of the pups already had low values ($F_{1,92}$ = 9.98, P = 0.002). Moreover, for recruitment calls, male young already had equal scores to that of adult males, whereas there was a clear difference between young and adult females (age*sex: $F_{1,18}$ = 10.45, P = 0.005). For terrestrial calls, young emitted calls with both higher peak frequency and more energy located at higher frequencies compared to adults.

Calls of adults and young also differed in the scores of the second principal component for aerial and terrestrial calls, but not recruitment calls (aerial: $F_{1,92}$ = 4.97, P = 0.03; terrestrial: $F_{1,13}$ = 14.51, P = 0.002; recruitment: $F_{1,18}$ = 1.20, P = 0.29). For aerial calls, individuals younger than six months had a little more modulated and longer calls compared to sub-adults and adults. After six months, calls showed little change regarding modulation and duration. For terrestrial calls, young exhibited lower amplitude ratio between the first and second dominant frequency band, which was much more apparent in males than females (age*sex: $F_{1,13}$ = 21.18, P < 0.001). The third principal component was influenced by age for

aerial calls ($F_{1,92} = 11.50$, $P = 0.001$), but not terrestrial ($F_{1,22} = 0.89$, $P = 0.35$) or recruitment calls ($F_{1,18} = 1.01$, $P = 0.32$). Young less than six months of age had, as for terrestrial calls, more energy at higher frequencies and slightly more noisy calls compared to adults. Remaining components were not influenced by age for any call type ($P > 0.10$ for all). Apart from the above mentioned effects, there was no influence of sex on any of the other principal components ($P > 0.20$ for all call types).

In contrast to calls emitted in low urgency contexts, we found very little effect of age on calls emitted in high urgency contexts. None of the principal component scores for aerial high urgency calls were influenced by age (PC1: $F_{1,17} = 0.69$, $P = 0.42$; PC2: $F_{1,17} = 0.62$, $P = 0.44$; PC3: $F_{1,17} = 0.34$, $P = 0.57$; PC4: $F_{1,17} = 0.61$, $P = 0.45$, table 2), and for recruitment high urgency calls, only the first component was affected (PC1: $F_{1,27} = 20.88$, $P < 0.001$; PC2: $F_{1,27} = 0.42$, $P = 0.52$; PC3: $F_{1,18} = 0.03$, $P = 0.86$; PC4: $F_{1,27} = 0.60$, $P = 0.45$, table 2). Young again had more energy located at higher frequencies and higher median peak frequency than adults. There was no influence of sex on any of the components ($P > 0.12$ for both call types).

Table 2. The effect of age on each of the principal components (pc) included in the univariate analysis of each call type. + represents change with age, and 0 represents no change. Alu = Aerial low urgency, Tlu = Terrestrial low urgency, Rlu = Recruitment low urgency, Ahu = Aerial high urgency, and Rhu = Recruitment high urgency.

call type	pc1	pc2	pc3	pc4	pc5
Alu	+	+	+	0	0
Tlu	+	+	0	0	0
Rlu	+	0	0	0	0
Ahu	0	0	0	0	
Rhu	+	0	0	0	

Discussion

The alarm calls of young meerkats were more or less structurally indistinguishable from those of adult calls when first produced, yet the discrimination of calls along the level of urgency was better than the discrimination of different predator types. Calls of both adults and young showed a high correct classification to low (predators far away) and high (predators closeby) urgency contexts, and a consistent change in acoustic structure along the level of urgency across predator types (for adult calls, see also Manser 2001). In contrast, whereas predator-specific calls given by adults showed a high correct classification, those given by young overlapped more and showed a correct assignment similar to that expected by chance. These results suggest that the adult-like structure of acoustic features encoding information about the level of urgency develops earlier than the structure of those features encoding information about specific predator types.

Since acoustic parameters encoding information about the level of urgency in meerkat alarm calls (see Manser 2001) are all features known to be associated with fear or anxiety in other animal vocalizations and human speech (Morton 1977; Papoušek 1989; Hauser 1993), it is reasonable to assume that the acoustic structure grading along the level of urgency may be a direct consequence of the caller's motivational state at the time of calling (Morton 1977;

Marler et al. 1992; Evans 1997). Because meerkat alarm calls seem to convey information about the level of urgency along a general rule, in contrast to the information about specific predator types (Manser 2001; this study), it has been suggested (Manser 2001) that such an alarm-call system might support the idea that motivational signals are the substrate from which referential signals evolve (Macedonia 1993). Our results showing that referential aspects of alarm calls change more over time provide additional support for this idea. Moreover, the high urgency growl calls emitted by very young pups clustered relatively separately from other high urgency predator-specific calls, suggesting that growl calls gradually develop into the other call types as young grow older. We also previously found that predator-specific calls appear much later in the repertoire of young than do non-specific calls (L. I. Hollén and M. B. Manser, unpublished data). Together, these findings suggest that producing and correctly pronouncing calls encoding referential information may require practice, and show similarities to that observed in human speech development, where children learn to attach specific meanings to different words (Locke & Snow 1997).

Although the calls of young showed relatively little discrimination between the different predator types, they were classified slightly better in high urgency than low urgency contexts. Compared to low urgency calls, high urgency calls also showed a high correct classification when the principal components explaining differences between adult calls were used to assign the calls of young and vice versa, suggesting that the structure of high urgency calls are already similar to those of adult calls. This was confirmed by the univariate analysis showing that high urgency calls underwent relatively little age-related modification. A similar pattern was found in ringtailed lemurs (*Lemur catta*), where aggressive calls typically noisy in structure, whether present or not at birth, were relatively adult-like in structure when they appeared in the repertoire (Macedonia 1993). One explanation for these findings could be that noisy calls are easier for young individuals to produce than are tonal calls, since it requires relatively little control over the vocal apparatus (e.g. Liebermann 1986). It has been suggested that in humans, an age-related increase in tonality of infant calls is likely to be brought about by an improvement of the subglottal air-pressure control as individuals grow (Boliek et al. 1996; Scheiner et al. 2002).

Our univariate analysis showed that the alarm calls of meerkats undergo slight but not substantial modification as individuals age, a form of vocal plasticity found in several other species. The calls of young meerkats were higher pitched than those of adults, similar to infant primates (e.g. Seyfarth & Cheney 1986; Gouzoules & Gouzoules 1989; Hammerschmidt et al. 1994, 2000), young rodents (Blumstein & Munos 2005; Randall et al. 2005), and human children (Scheiner et al. 2002). Changes in fundamental and peak frequency related parameters determining the pitch are likely to reflect physical maturation due to the increasing length of the vocal tract and the size of the resonance cavities as individuals age and grow (Fitch & Hauser 1995; Fischer et al. 2002). Why young males, in contrast to females, emitted calls of equally low frequencies as that of adults remains unclear at this stage. Similar maturational changes may be responsible for the increase in amplitude of the first dominant frequency band relative to that of the second band, and the downward shift of the main energy from higher to lower frequencies with increasing age. In human infants, however, an increase in fundamental frequency (Banse & Scherer 1996; Protopapas & Lieberman 1997), increase in call duration and an upward shift in energy from lower to higher frequencies (Scheiner et al. 2002) were also found during increased arousal. If young meerkats, due to their higher vulnerability, experience higher arousal than adults at the time of an alarm call, this might be responsible for some of the observed differences. However, this remains to be investigated.

To conclude, young meerkats seem predisposed to utter alarm calls with the same general features as those of adults from an early age but nevertheless undergo gradual modification during development. Adult-like features related to predator-specific information

seem to develop at later ages than those encoding information about perceived urgency. The developmental trajectories of alarm-call production found in meerkats extend the already existing parallels between the properties of speech development in humans and the development of call production in many nonhuman primates. To our knowledge, however, this is the first study on nonhuman animals to consider the specific information conveyed by different alarm calls when studying their development.

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APPENDIX 1: ACOUSTIC PARAMETERS MEASURED BY LMA

Parameters included in the analyses of low urgency calls are indicated with * and those of high urgency calls with †. The number of parameters included for each call type and urgency level varies (see Table 1)

Parameter	**Description**
duration*†	Duration (ms)
q1st*†	Start frequency (beginning of the call) of the 1st quartile of distribution of frequency amplitudes (Hz)
q1end*	End frequency (end of the call) of the 1st quartile of distribution of frequency amplitudes (Hz)
q1min*†	Minimum frequency of the 1st quartile of distribution of frequency amplitudes, across all time segments (Hz)
q1med*†	Median frequency of the 1st quartile of distribution of frequency amplitudes, across all time segments (Hz)
q1maloc*†	Location of the maximum frequency in the 1st quartile of distribution of frequency amplitudes (between 0-1)
q2st*	Start frequency of the 2nd quartile of distribution of frequency amplitudes (Hz)
q2min*†	Minimum frequency of the 2nd quartile of distribution of frequency amplitudes, across all time segments (Hz)
q2med*†	Median frequency of the 2nd quartile of distribution of frequency amplitudes, across all time segments (Hz)
q2maloc*	Location of the maximum frequency in the 2nd quartile of distribution of frequency amplitudes (between 0-1)
df1st*	Start frequency of first dominant frequency band (Hz)
df1max*	Maximum frequency of the first dominant frequency band, in all time segments (Hz)
df1min*†	Minimum frequency of the first dominant frequency band, across all time segments (Hz)
df1med*†	Median frequency of the first dominant frequency band, across all time segments (Hz)
df1chfre*†	Number of changes between original and floating average curve in first dominant frequency band (local modulation)
df1maloc*	Location of the maximum frequency in the first dominant frequency band (between 0-1)
df1trfak*†	Slope of the linear trend of the first dominant frequency band (global modulation)
df1fretr*†	Alternation frequency between first dominant frequency band and linear trend
df2max*	Maximum frequency of the second dominant frequency band, in all time segments (Hz)
df2med*	Median frequency of the second dominant frequency band, across all time segments (Hz)
diffmean*†	Average difference between first and second dominant frequency band (Hz)
dffreq*	Average number of dominant frequency bands
ampratio1*†	Amplitude ratio between first and second dominant frequency band
pfst*	Start peak frequency (Hz)
pfmin*	Minimum peak frequency across all time segments (Hz)
pfmed*†	Median peak frequency across all time segments (Hz)
pftotmax*†	Frequency of the total maximum amplitude (Hz)
pfmaloc*†	Location of the maximum peak frequency (between 0-1)
pftrfak*†	Slope of the linear trend of the peak frequency (global modulation)
pftrfre*†	Alternation frequency between the peak frequency and linear trend (Hz)
meanhnr*	Mean harmonic to noise ratio (1 = no noise)
maxhnr*	Maximum harmonic to noise ratio (1 = no noise)

CHAPTER 5

Experience with predators has little influence on alarm-call production and olfactory predator recognition in meerkats (*Suricata suricatta*): a comparison between free-living and captive populations

To be submitted

CHAPTER 5

Experience with predators has little influence on alarm-call production and olfactory predator recognition in meerkats (*Suricata suricatta*): a comparison between free-living and captive populations

Linda I. Hollén

Verhaltensbiologie, Zoologisches Institut, Universität Zürich, Winterthurerstrasse 190, 8057 Zürich, Switzerland

Abstract

Performing correct anti-predator behaviour is crucial for prey to survive, but such costly behaviour may be lost when species find themselves isolated from predators. However, the degree to which anti-predator behaviour depends upon experience and the specificity of cues evoking the behaviours, may influence how quickly they are lost. Wild meerkats (*Suricata suricatta*) live under a high predation pressure and have evolved a sophisticated alarm call system consisting of predator specific and non-predator specific alarm calls, with predator specific calls simultaneously conveying information about response urgency. In this study, we investigated the production and usage of alarm calls and olfactory predator recognition in captive populations of meerkats, and compared the results to earlier findings in wild populations. All alarm calls that have been documented in the wild also occurred in captivity and were given in broadly similar contexts. The acoustic structure, however, differed slightly from that observed in the wild. Furthermore, without experience of odours from predators, captive meerkats seemed to distinguish between faeces of potential predators (carnivores) and non-predators (herbivores). Together, these results suggest that, as in the wild, alarm-call production, the use of alarm calls in appropriate contexts, and olfactory predator recognition are relatively independent of experience, and can be retained in captive populations lacking exposure to predators.

Introduction

Predation is a major selective force leading to numerous behavioural and morphological adaptations in prey (Lima & Dill 1990). Yet, how does anti-predator behaviour change in the absence of predators? Isolation from predators may happen on islands (Berger et al. 2001; Blumstein 2002) but also in captivity (Griffin et al. 2000). Comparing wild and captive populations of the same species provides a powerful approach to investigate a species' capabilities in terms of anti-predator behaviour. Because anti-predator behaviour can be costly, for example in terms of reduced reproductive output or time allocated to vigilance rather than energy intake (reviewed in Lind & Cresswell 2005), we might expect it to be lost in predator-free populations (Coss 1999). To really understand how animals respond to isolation from predators, however, we need to identify the degree to which anti-predator behaviour is experience-dependent. Behaviours which are largely dependent upon experience may change rapidly following the loss of predators, whereas experience-independent behaviours may persist for several generations after isolation (Coss 1999; Blumstein 2002). This idea was supported by a recent study on wild and captive sifakas (*Propithecus verreauxi*) showing that both groups produced the same alarm call types, but used and perceived them in strikingly different ways (Fichtel & van Schaik 2006). It is generally believed that experience influences the ability to correctly use and respond to alarm calls in wild non-human primates, whereas alarm-call production is more or less independent of experience (Seyfarth & Cheney 1980, 1986, 1997; Mateo 1996; Ramakrishnan & Coss 2000; Fischer et al. 2000; McCowan et al. 2001).

The degree to which anti-predator behaviour persists or is lost may also depend on the type of cues evoking the behaviour. In tammar wallabies (*Macropus eugenii*), responsiveness to visual cues which were shared by several predator types was preserved, whereas acoustic recognition which depends on relatively specific cues was not, suggesting that cues which show convergent features may be more likely to persist (Blumstein et al. 2000). Like visual cues, olfactory cues can also show convergent features. Different species of carnivores, for example, produce similar sulphurous compounds as a by-product of the digestion of animal proteins (Nolte et al. 1994). Olfactory predator recognition might thus be expected to persist despite a lack of experience with such cues. Yet, even though many animals show anti-predator behaviour in response to chemical cues from predators (Barreto & MacDonald 1995; Ward et al. 1997; Blumstein et al. 2002; Pillay et al. 2003; Monclús et al. 2005), there is no general agreement as to whether this recognition is dependent upon experience or not.

In this study, we investigated the influence of predator experience on alarm-call production, alarm-call usage, and olfactory predator recognition in meerkats (*Suricata suricatta*). We studied six captive populations, and compared the results to those obtained in earlier studies on free-living animals (Manser 2001; L.I. Hollén & M.B. Manser, unpublished data). Meerkats are cooperatively breeding mongooses which normally inhabit arid regions of Southern Africa (Clutton-Brock et al. 1999a). Compared to captive animals, which live in a relatively predator free environments, free-living meerkats live under extreme predation pressure and are predated upon by several species of raptors, mammalian predators and snakes (Clutton-Brock et al. 1999b). They exhibit a sophisticated alarm call system consisting of several call types that are not specifically related to a single predator type, and alarm calls emitted only in response to specific predator types. Additionally, the acoustic structure of predator type specific calls simultaneously encodes information about the signaller's perception of response urgency (Manser 2001). Olfactory cues, such as urine, faecal and hair samples of predators, have been shown to elicit behavioural and vocal responses in free-living meerkats (Manser 2001).

Using observations on alarm calling behaviour and experimental presentations of olfactory cues, we investigated potential differences in anti-predator behaviour between

captive and wild populations of meerkats. We recorded whether captive meerkats produced all alarm call types that have been observed in the wild, and in which contexts they were used. We also tested whether these calls were similar in acoustic structure to those emitted in the wild. We finally investigated whether captive meerkats, as wild meerkats, were able to distinguish between olfactory cues of potential predators and non-predatory odours by presenting them with faeces of carnivores and herbivores.

Methods

Study sites and subjects

Between August 2004 and December 2005, we studied six captive populations of meerkats living in different zoos situated in Switzerland (Basel), Germany (Cologne, Karlsruhe, Hannover, Osnabrück) and Ireland (Dublin). Observations and experiments were conducted during 2-3 days in each zoo. Group size varied between 6 and 16 individuals, which is within the range of that observed in the wild (Clutton-Brock et al. 1999a). All six populations had access to both indoor and outdoor enclosures. Except for young offspring in two groups, all mature individuals were according to birth records at least one year old and born in captivity. Individual identification was not feasible, except in one zoo where individuals were distinctly marked with hair dye.

Free-living meerkats were studied during 2003 and 2004 in 13 well habituated (close observation within 1m) groups in the South African part of the Kalahari Desert (26º58´S, 21º49´E) (study site details provided in Clutton-Brock et al. 1999a). Each animal was marked for individual identification with hair dye or hair cuts applied to their fur unobtrusively during sunning at the morning sleeping burrow. The exact age of all individuals were known because they had been monitored since birth.

Recording methods

To determine whether captive meerkats use the same alarm calls as has been described for wild meerkats, whether these calls are used in similar contexts and whether the acoustic structure differs, we recorded alarm calls emitted in response to natural encounters on an ad libitum basis. We recorded alarm calls at a distance of two to four meters from the caller (44.1 kHz sampling frequency) using a Sennheiser directional microphone (ME66/K6 with a MZW66 pro windscreen; frequency response 40–20000 Hz ± 2.5 dB, Old Lyme, CT, U.S.A.) connected to a Marantz PMD-670 solid state recorder (D&M Holding, Inc., Kanagawa, Japan). The stimuli eliciting the alarm calls were spoken onto the tape. All alarm calls were recorded outdoors and from adult individuals. Calls were transferred to a PC (sampling frequency: 44.1 kHz; resolution: 16 bit) and visually inspected using Cool Edit 2000 (Syntrillium, Phoenix, AZ, U.S.A.). For acoustic analysis, we only chose calls with sufficiently high quality. Due to high level of background noise in many zoos, several of the calls had to be excluded from further analyses.

Experimental presentation of olfactory cues

To investigate whether captive meerkats are able to recognize predators through olfactory cues, we presented individuals with faeces from carnivores (potential predators) and herbivores (non-predators). For the carnivore category, we used faeces from the African lion (*Panthera leo*), Siberian tiger (*Panthera tigris*), snow leopard (*Unica unica*) and cheetah (*Acinonyx jubatus*). For the herbivore category, we used faeces from the impala (*Aepyeros*

melampus), common duiker (*Sylvicapra grimmia*), scimitar horned Oryx (*Oryx dammah*) and alpaka (*Lama pacos*). Faeces from some species were presented in more than one zoo. Each population was presented with one sample of carnivore faeces and one sample of herbivore faeces, with at least 2 hours in between. Samples were kept in a freezer and defrosted shortly before use. Presentations of herbivore faeces always preceded presentations of carnivore faeces, because carnivore faeces typically elicited a strong reaction which might have influenced subsequent reactions. All faeces were presented in the outdoor enclosures and removed immediately after testing.

We recorded the behavioural responses with a Sony digital video camera DCR-TRV50E and alarm calls with the same microphone arrangement as above. The recorded alarm calls were used for acoustic analysis. We analysed the video tapes using frame-by-frame analysis (12.5 frames/s) in Microsoft Windows Movie Maker version 5.1. We obtained the following measurements: (i) the total duration a group spent inspecting the faeces, and (ii) the length of alarm call bouts. We used the group response (first individual to sniff/call and last individual to leave/call) since the identity of individuals could not always be determined. Since individuals repeatedly returned to sniff the faeces after an initial inspection, we defined the end of a response as the time when 1 minute passed without any animal coming back.

Acoustic analysis

We first conducted a fast Fourier transformation (1024-point FFT) of all calls using AVISOFT-SASLab pro 4.38 (R. Specht, Berlin, Germany). We used a frequency range of 8 kHz (frequency resolution 14Hz) or 11.025 kHz (frequency resolution 28 Hz) depending on call type. Time resolution was 2 and 1.45 ms respectively (98.43% overlap). The resulting frequency – time spectra were analysed with LMA 2005 (developed by K. Hammerschmidt), a software tool that extracts a set of call parameters from acoustic signals (Schrader & Hammerschmidt 1997). A list of the parameters we used is given in Appendix A.

In brief, we first calculated parameters describing the first two dominant frequency bands (dfb). In tonal calls, these bands represent the fundamental frequency and its harmonics whereas in atonal signals, they reflect the frequency peaks with the highest energy. Secondly, we determined the distribution of spectral energy measured as the first and second quartiles of the distribution of frequency amplitudes (dfa) in the spectrum. Thirdly, we calculated the local and global modulation of the first dfb and dfa. Fourthly, we determined the location and the modulation of the peak frequency (the frequency with the highest amplitude in a time segment). Finally, we measured temporal parameters such as call duration and temporal location of the maximum peak frequency (details of parameters provided in Schrader & Hammerschmidt 1997). We included 3 call types in the analysis: calls given in response to objects in the air (aerial calls), calls emitted in response to moving objects (moving animal call; see Manser 2001) and calls emitted in response to faeces presentations (recruitment calls; see Manser 2001).

Statistical analyses

Because of differences in the amount of time spent observing each population (due to factors such as bad weather, too much disturbance, limited access etc), we were not able to record alarm calls in a standardized way across all zoos and therefore present the data on alarm-call usage qualitatively instead of quantitatively. All statistical analyses were conducted in R for Microsoft Windows version 2.2.1 (R Development Core Team 2005; URL: http://www.r-project.org), using the software packages ‘MASS’ (Venables & Ripley 2002), ‘Hmisc’ (Harrell et al. 2006), ‘Design’ (Harrell et al. 2005) and ‘ipred’ (Peters & Hothorn 2004). Assumptions of multi- and univariate normality and homogeneity of variances were fulfilled.

For the analyses on acoustic differences, we first replaced missing values among the acoustic parameters using a multiple imputation approach (Little 2004). A range of values (n = 20) for each missing observation were imputed and the missing values replaced with the mean of these estimates (function aregImpute in 'Hmisc'). We then used discriminant function analysis (function lda in 'MASS') to determine classification probabilities of alarm calls emitted in captivity and in the wild. To avoid correlated predictor variables, we first conducted principal component analysis based on a correlation matrix (function princomp in 'MASS') and used the unrotated principal components (explaining 70-80% of the original variation) as classifiers in the DFA. For external validation, we used 10-fold cross validation (function errorest in 'ipred'). Since sample sizes of calls from captive meerkats were relatively low, we chose a random subset of calls from free-living meerkats to minimise a possible bias in our results. We calculated assignment probabilities expected by chance using a bootstrap approach. Taking into account the initial sample sizes in the actual data, random numbers were assigned to each call class. Chance probabilities from 1000 repeats are presented with ± 1 SE. On average, assignment probabilities equal to or greater than that obtained in the discriminant analyses were generated by chance in less than 10% of all bootstrap repeats. To test for univariate differences within each call type, we conducted a set of general linear models (function lm in 'MASS') with unrotated principal components as response variables in all models. Tests were 2-tailed and significance level set at $P < 0.05$. We analysed the inspection time and call bout length in response to faeces presentations with Wilcoxon tests (function wilcox.test in 'MASS'). V is the derived test statistic when applying this function in R.

Results

Alarm-call usage

All alarm calls that have been documented in the wild (Manser 1998; Manser 2001) were also recorded in captivity. However, in some zoos, alarm calling was never observed. The most reliable contexts that elicited alarm calls were the sightings or sounds of airplanes, helicopters, zeppelins and non-dangerous birds such as crows (*Corvus corone*). The alarm calls emitted in these contexts had the same general structure as aerial medium urgency or alert calls recorded in the wild (Fig. 1a). Aerial calls are typically elicited by raptors in the wild, but occasionally also by non-dangerous birds such as vultures (*Torgos tracheliotus* and *Gyps africanus*) or grouse (*Pterocles sp.*) or the occasional plane flying over. Low risk situations such as non-dangerous birds closeby or raptors far away, however, typically elicit alert calls in the wild (Manser 2001). In captivity, zeppelins in particular elicited a noisy barking call. In the wild, barking calls are emitted in extremely high urgency situations such as raptors perched closeby or terrestrial predators coming very close (Manser 2001).

Alarm calls other than aerial calls were relatively uncommon in captivity. Terrestrial alarm calls of both low and high urgency character were only heard in one zoo, where a keeper walked past the enclosure with a dog. All meerkats showed an intense response and continued emitting alarm calls for at least 15 minutes after the dog disappeared. Free-living meerkats encountering dogs show similarly strong responses (pers. obs). The dog also elicited the so called moving animal call, a call type which is in the wild emitted in response to dangerous or non-dangerous animals moving and also foreign meerkats approaching the group (Manser 2001). In fact, one captive group once elicited this call in response to reflections of their own mirror images, possibly interpreted as foreign meerkats approaching. Moving animal calls were also commonly emitted in response to animal keepers bringing food or visitors walking past. In response to sudden disturbances, captive meerkats emitted

the so called panic call, which typically caused others to seek shelter. The same is observed in the wild, with meerkats typically running below ground in response to panic calls, commonly elicited by aerial and terrestrial predators closeby making sudden moves (Manser 2001). Finally, the alarm calls elicited in response to the faeces presentations resembled the so called recruitment low urgency call elicited in similar contexts in the wild (Fig. 1b). These calls have been termed recruitment calls since they cause recruitment of other group members to the site (Manser 2001; Manser et al. 2001). However, in contrast to free-living meerkats, captive animals seldom emitted the high urgent form of these calls.

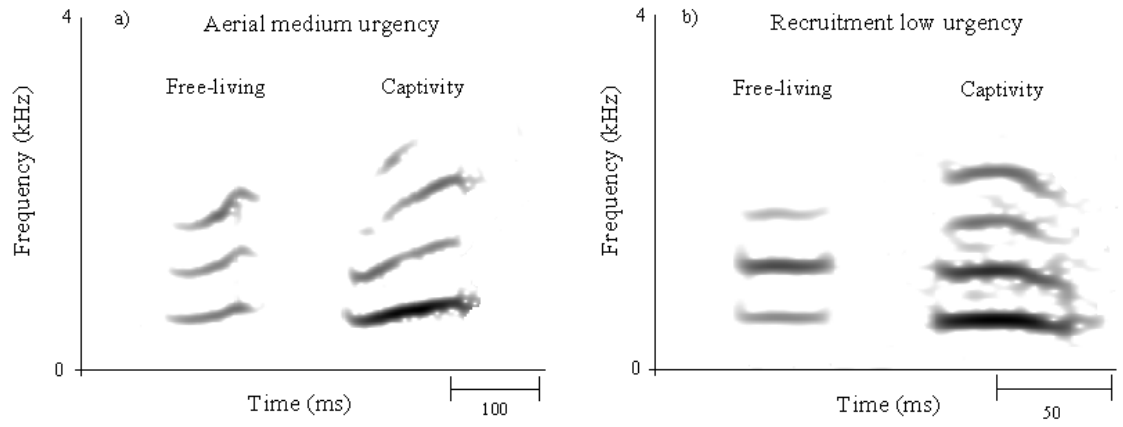

Figure 1. Examples of aerial medium urgency calls (a) and recruitment low urgency calls (b) emitted by free-living and captive meerkats in response to aerial objects and olfactory predator cues respectively.

Acoustic differences

Aerial calls

Aerial calls of captive and wild animals could accurately be distinguished based on their acoustic structure. With 3 principal components (extracted from 14 parameters), aerial calls of captive (N = 6) and free-living individuals (N = 10) showed a correct classification of 82% after cross validation (88% before validation), which is greater than the 50 ± 0.06 expected by chance (Fig. 2). Univariate analysis showed that only the first component explained the difference between the two groups (PC1: $F_{1,14} = 20.61$, $P < 0.001$; PC2: $F_{1,14} = 0.93$, $P = 0.35$; PC3: $F_{1,14} = 0.08$, $P = 0.78$). Parameters highly associated with this component were the median frequency in the first quartile of the distribution of frequency amplitudes, the median frequency of the first dominant frequency band and the median peak frequency. The calls of captive animals had higher fundamental frequency and the majority of energy located at higher frequencies than the calls of free-living meerkats.

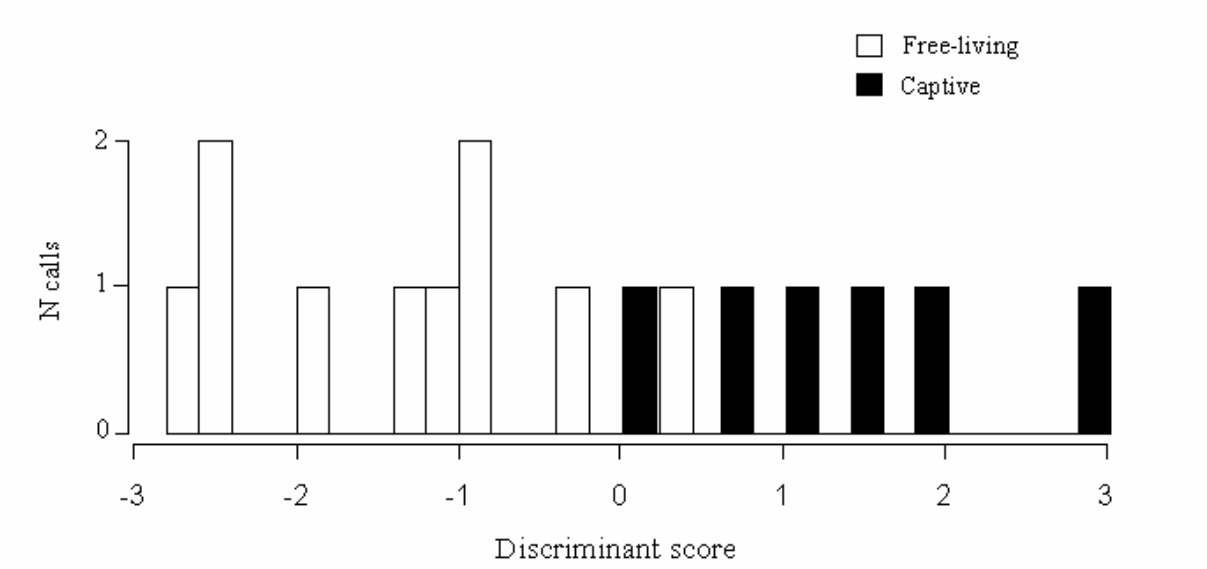

Figure 2. Classification results from the discriminant function analysis on aerial calls of free-living and captive meerkats. $N_{captive} = 6$, $N_{free\text{-}living} = 10$.

Moving animal calls

Like aerial calls, moving animal calls emitted in captivity differed in their acoustic structure from those emitted in the wild. Calls of captive (N = 7) and wild (N = 10) animals showed a correct assignment of 71% after cross validation (88% before), compared to 51 ± 0.06 expected by chance (3 principal components extracted from 12 parameters). Only the first component was responsible for this difference (PC1: $F_{1,15} = 12.54$, $P = 0.003$; PC2: $F_{1,15} = 0.01$, $P = 0.92$; PC3: $F_{1,15} = 0.32$, $P = 0.58$). Captive meerkats emitted calls with a higher median peak frequency and total maximum amplitude compared to wild ones.

Recruitment calls

Although the recruitment calls emitted in response to faeces presentations sounded similar to those in the wild, the discriminant analysis showed that their acoustic structure differed. With 5 principal components (25 parameters), the calls showed a correct classification of 81% after cross validation (93% before), compared to the 50 ± 0.04% expected by chance (captivity: N = 14; wild: N = 13). Since some of the calls from captive individuals looked spectrographically very similar to terrestrial medium urgency calls emitted in the wild, we included a set of these calls (N = 15) in the analysis to see if there was any overlap between them. This yielded, after cross validation, a correct assignment of 71% (83% before), higher than the 34 ± 0.02 expected by chance. Even though the three call types were distinctive (Fig. 3), terrestrial calls were more often misclassified to recruitment calls emitted in captivity than to those emitted in the wild (27% versus 7%). The recruitment calls emitted in the wild and captivity were, however, misclassified to terrestrial calls at the same rate (14% versus 15%).

Univariate analysis showed that the first 3 principal components were responsible for the differences between the three call types (terrestrial calls included) (PC1: $F_{2,49} = 5.97$, $P = 0.005$; PC2: $F_{2,49} = 14.06$, $P < 0.001$; PC3: $F_{2,49} = 11.24$, $P < 0.001$; PC4: $F_{2,49} = 1.00$, $P = 0.38$; PC5: $F_{2,49} = 0.06$, $P = 0.94$). Acoustic parameters highly associated with these components were the median frequencies of the first two dominant frequency bands, parameters describing the distribution of frequency amplitudes, the global modulation of the first dominant frequency band and peak frequency and call duration. Captive meerkats

emitted calls with higher fundamental frequency, more energy located at lower frequencies, less modulation and of longer duration than free-living individuals. Fundamental frequency and frequency amplitude values were closer to that of terrestrial medium urgency calls than recruitment low urgency calls recorded from wild animals.

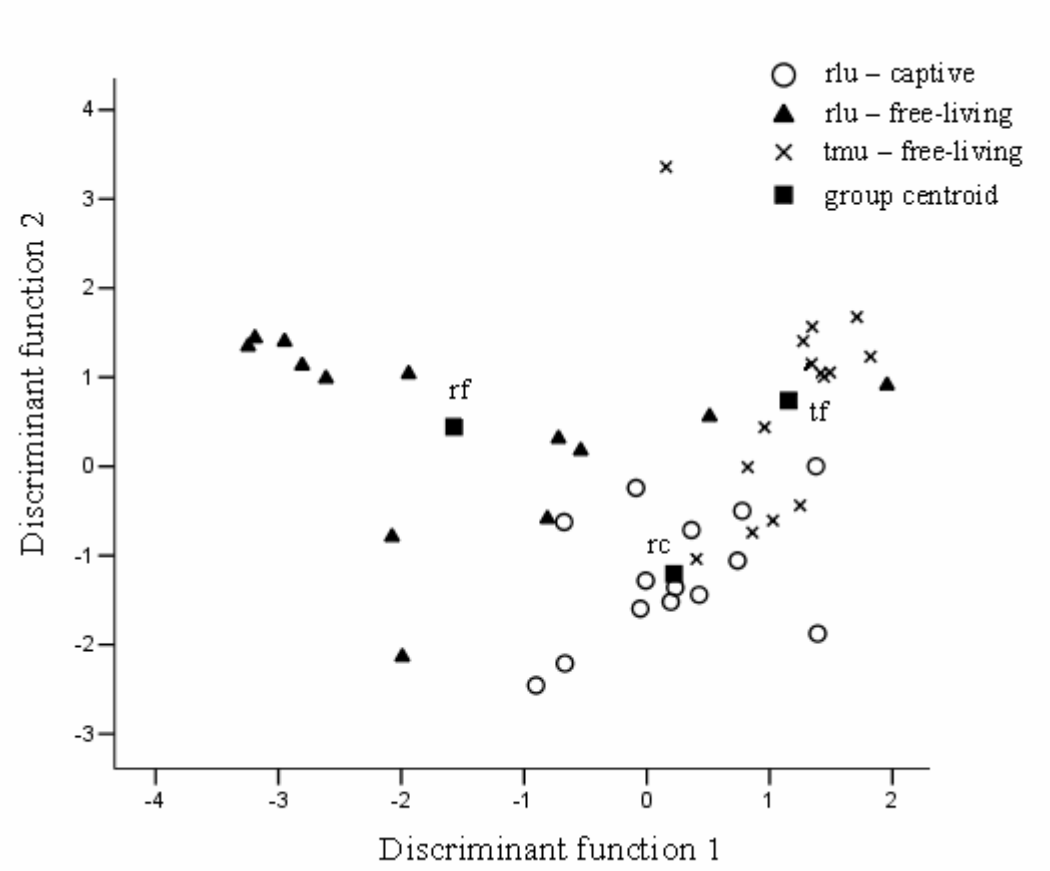

Figure 3. Classification results from the discriminant function analysis on recruitment low urgency calls (rlu) emitted in response to carnivore faeces in captivity (rc, N = 14), and hair samples of the African wildcat in the wild (rf, N = 13). Terrestrial medium urgency calls (tmu) emitted by free-living meerkats in response to mammalian predators were also included (tf, N = 15).

Olfactory predator recognition

In all cases, both carnivore and herbivore faeces were inspected, but carnivore faeces for a much longer time compared to herbivore faeces (carnivore: 124 ± 61 sec; herbivore: 20 ± 19 sec; Wilcoxon: $V_5 = 21$, $P = 0.03$, Fig. 4a). Carnivore faeces elicited calling in all 6 presentations compared to 4 out of 6 in response to herbivore faeces. Carnivore faeces, however, tended to elicit much longer bouts of alarm calling than herbivore faeces, which typically elicited only one or two calls (carnivore: 179 ± 96 sec; herbivore: 21 ± 11 sec; Wilcoxon: $V_3 = 10$, $P = 0.07$, Fig. 4b). These results are similar to that observed in response to olfactory cues in the wild. Hair samples of one of their main predators, the African wildcat (*Felis lybica*), typically elicit long bouts of calling and recruitment of the rest of the group. In contrast, hair samples of the non-dangerous Cape ground squirrel (*Xerus inauris*) are, if at all, inspected only briefly and do not elicit any alarm calls (Graw 2005).

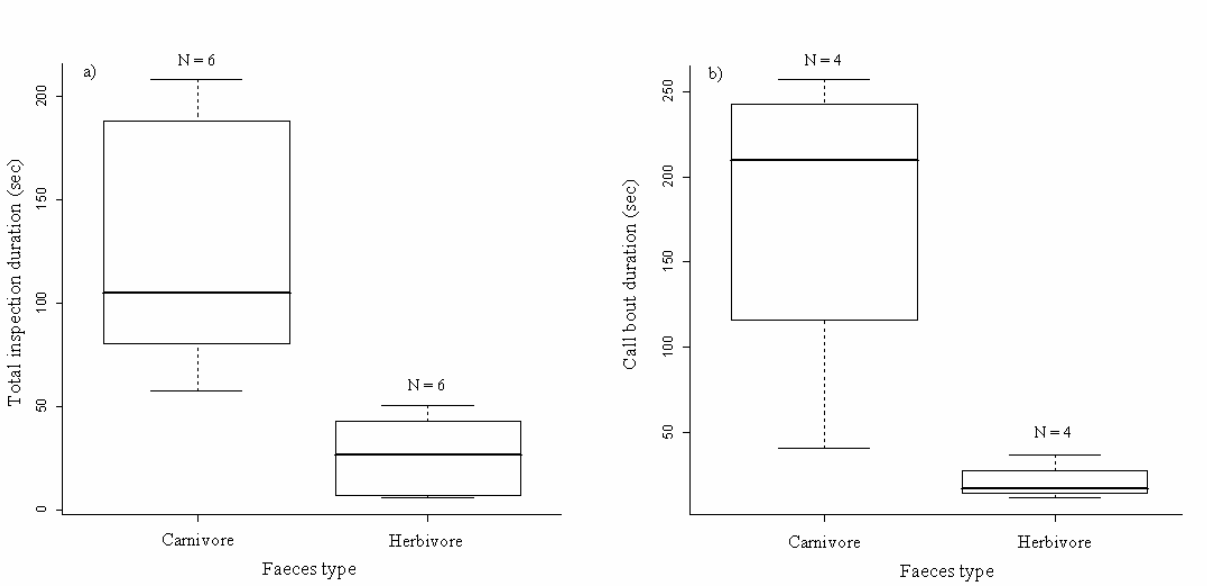

Figure 4. The time that captive meerkats spent inspecting stimuli (a) and alarm calling (b) in response to presentation of carnivore and herbivore faeces. Analyses were conducted on group level, thus sample sizes reflect the number of groups. Only those groups that called in response to both types of faeces were included in the analysis of call bout duration.

Discussion

In wild meerkats, the production of alarm calls with adult-like features is largely independent of experience, whereas the use of these calls in the correct contexts and olfactory predator recognition seem to depend on a mixture of relatively non-learned components and gradual modification as a result of experience (L.I. Hollén & M.B. Manser, unpublished data). If behaviours that are relatively independent upon experience change slowly following the loss of predators (Blumstein 2002), we might expect alarm-call production, alarm-call usage and olfactory predator recognition to persist in captive environments if not enough evolutionary time has passed for a response to the loss of predators (see Blumstein et al. 2000).

Supporting this, we found that all alarm calls that have been recorded from wild meerkats (Manser 1998; Manser 2001) were emitted by captive meerkats on one or several occasions, albeit not in all zoos. It may be that alarm calling in some zoos but not others reflects differences in the time spent observing each population or variation in the presence of disturbances. Nevertheless, our observations suggest that captive meerkats exhibit the same vocal repertoire of alarm calls as wild meerkats do. Similar findings were obtained in sifakas, where captive animals exhibited the same alarm call system as wild animals (Fichtel & van Schaik 2006). Most call types emitted by captive meerkats were also emitted in contexts resembling those observed in the wild. However, alarm calls normally given to raptors in the wild were often given to planes and non-dangerous birds. These results are similar to those found in vervet monkeys, where the nature of eliciting stimuli varies more widely in captivity and planes often elicit eagle alarms (Brown et al. 1992). Yet, such a transfer may be considered a normal adaptive process since wild animals may also change their alarms in new environments (Cheney & Seyfarth 1990). It is also consistent with wild meerkats (L.I. Hollén & M.B. Manser, unpublished data) and vervets (Cheney & Seyfarth 1990) sometimes over-generalizing aerial alarms to other flying objects such as planes and harmless birds. Probably because captive animals mainly encounter harmless aerial stimuli, as raptors seldom fly over (pers. obs), aerial alarm calls are mainly emitted in such contexts. Such behaviour may have

persisted in captivity because animals are still exposed to some stimuli with features broadly similar to predators in the wild (Blumstein et al. 2000, 2006).

Based on their acoustic structure, however, calls of captive and free-living meerkats were clearly distinguished using discriminant analyses. Compared to free-living individuals, captive ones generally emitted calls with higher fundamental frequency and more energy located at higher frequencies, except for recruitment calls where more energy was located at lower frequencies. Recruitment calls of captive individuals were also of longer duration. Higher fundamental frequency and energy at higher frequencies may seem counter-intuitive. Higher values are typically associated with individuals of younger age and smaller body size (Hammerschmidt et al. 2000; Fischer et al. 2002), but captive individuals were all adults and commonly bigger than those in the wild (pers. obs). It is however possible that, due to their bigger size, captive meerkats have a greater lung capacity and can increase the subglottal pressure, which in turn can lead to an increase in fundamental frequency and call duration (Hsiao et al. 1994; Hammerschmidt et al. 2000, 2001). A rise in fundamental frequency, an upward shift in energy from lower to higher frequencies and an increase in call duration have also been shown in humans (Banse & Scherer 1996; Scheiner et al. 2002) and non-human primates (Fichtel et al. 2001; Rendall 2003) during increased arousal. However, given that recruitment calls were of both longer duration (bigger size and/or high arousal) and had more energy at lower frequencies (bigger size and/or low arousal), a combination of morphology and arousal may be a plausible explanation for the observed differences. Yet, whether captive and free-living meerkats experience differences in arousal, and whether this is due to differences in predator experience or perhaps contextual differences, remains to be investigated. It is also possible that the observed differences may be based on differences in the acoustic environment between wild and captive populations. Zoo environments are typically very noisy, whereas the level of background noise in the wild is relatively low. It has been shown in some bird species that amplitude and frequency parameters of song can be adjusted depending on the background noise level (Slabbekoorn & Smith 2002; Brumm 2004).

Finally, the results from our faecal presentations suggest that captive meerkats growing up in a relatively predator free environment can recognize and respond adaptively to odours signaling the presence of potential predators, similar to that of free-living individuals (Manser 2001). Captive meerkats treated faeces of carnivores and herbivores differently by inspecting carnivore faeces for a longer time compared to non-predatory odours of herbivores. Carnivore faeces also elicited longer bouts of alarm calling, and despite a few structural differences, these alarm calls resembled the recruitment calls emitted in response to deposits such as faeces or hair samples of predators in the wild. Although experience-independent odour recognition is present in some species (e.g. Calder & Gorman 1991; Coss 1999; Ward et al. 1997; Barreto & MacDonald 1999; Monclús et al. 2005), predator-naïve individuals of other species seem to modify their behaviour in response to olfactory cues through learning (Berger et al 2001; Blumstein et al. 2002; Mathis et al. 1993; 1996). Even in species where learning is required, however, odour recognition is often acquired rapidly (Chivers & Smith 1998; Berger et al. 2001; Larson & McCormick 2005; Ferrari et al. 2005).

We previously found that although young meerkats often do not respond to hair samples of a predator and only start emitting appropriate alarm calls at around two months of age, the correct use of these calls were acquired more rapidly than other call types (L.I. Hollén & M.B. Manser, unpublished data). This suggests that experience, albeit relatively little, may be needed to recognize hair samples of predators as dangerous. So why do captive adults which are not likely to have had experience with odours of predators react so strongly to olfactory cues? It is possible that even if behavioural responses to hair samples are absent in young wild animals, it does not necessarily imply that the young do not recognize the odour (Ydenberg & Dill 1986; Monclús et al. 2005). In fact, even very young pups emitted calls in

response to the hair but calls rather resembled contact calls emitted in foraging contexts, suggesting that young might recognize the hair but do not yet know which calls to emit. It could also be that faeces show more convergent features than hair samples of predators and that meerkats might have been selected to recognize such cues relatively independent of experience. It is possible that captive animals still investigated herbivore faeces and sometimes emitted a few calls because the cost of making a mistake for captive animals in a relatively predator-free environment is less than for wild animals and that captive animals are more 'relaxed' and therefore less likely to discriminate.

To conclude, captive meerkats with relatively little experience of predators can recognize potential predators by means of olfactory cues, they still exhibit the same alarm call system as that observed in the wild and the contexts in which alarm calls are given largely resemble those in the wild. Most of the basic call structures have been retained, and alarm calling to objects such as planes may not be surprising given the environment in which they are living and the fact that wild meerkats also respond to planes occasionally passing by. Our results support the idea that anti-predator behaviour which require relatively little experience for proper performance can persist in populations living in the absence of predators.

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CURRICULUM VITAE

PERSONAL DATA

Surname	HOLLÉN
First names	Linda Irene
Date of birth	20.06.1977
Nationality	Stockholm, Sweden

EDUCATION

1993 – 1996	Rättvik Agricultural upper secondary school, Rättvik, Sweden
1996 – 1997	Studies of Biology, Chemistry, Physics, Mathematics and English (Scientific base year) at the Municipal adult education, Leksand, Sweden
1997 – 2000	B.Sc. in Biology at the University of Stockholm & the University of Umeå, Sweden
2001	M.Sc. in Biology at the University of Stockholm, Sweden Master thesis on: "Take-off performance and compensatory responses to experimentally increased wing loading in tree sparrows (*Passer montanus*)", under the supervision of Dr. Sven Jakobsson and Dr. Johan Lind
2002 – 2006	PhD at the Institute of Zoology, Animal Behaviour, University of Zürich, Switzerland under the supervision of Prof. Dr. Marta Manser on " Development of alarm call production, usage and responses in meerkats (*Suricata suricatta*)".

PUBLICATIONS

Included in thesis:

Hollén, L.I. & Manser, M.B. (2006) Ontogeny of alarm call responses in meerkats (*Suricata suricatta*): the roles of age, sex and nearby conspecifics. *Animal Behaviour* d*oi:10.1016/j.anbehav.2006.03.020*

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Other publications:

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CURRENT POSITION

2002 – 2006	PhD position at the Zoological Institute, Animal Behaviour department, University of Zürich, Switzerland
2006 - 2007	Research assistant position at the Zoological Institute, Animal Behaviour department, University of Zürich, Switzerland with Prof. Dr. Marta Manser